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A REVISION OF THE GENUS
CHLOROSPATHA (ARACEAE)^{1,2}

Thomas B. Croat³ and Lynn P. Hannon†

ABSTRACT

This is the first revision of the genus *Chlorospatha* Engl. (Araceae) since Michael Madison's 1981 treatment. The genus consists of three sections, two of which are newly established: *Chlorospatha* sect. *Occidentales* Croat & L. P. Hannon and *Chlorospatha* sect. *Orientales* Croat & L. P. Hannon. Included are 69 taxa (68 species and one variety) for Central and South America, of which 45 are new to science. These include 39 newly described species: *C. bayae* Croat & L. P. Hannon, *C. boosii* Croat & L. P. Hannon, *C. bullata* Croat & L. P. Hannon, *C. caldasensis* Croat & L. P. Hannon, *C. caliensis* Croat & L. P. Hannon, *C. carchiensis* Croat & L. P. Hannon, *C. cedralensis* Croat & L. P. Hannon, *C. chocoensis* Croat & L. P. Hannon, *C. congensis* Croat & L. P. Hannon, *C. engleri* Croat & L. P. Hannon, *C. giraldoi* Croat & L. P. Hannon, *C. grayumii* Croat & L. P. Hannon, *C. hannoniae* Croat, *C. hastata* Croat & L. P. Hannon, *C. huilensis* Croat & L. P. Hannon, *C. jaramilloi* Croat & L. P. Hannon, *C. limonensis* Croat & L. P. Hannon, *C. litensis* Croat & L. P. Hannon, *C. longiloba* Croat & L. P. Hannon, *C. maculata* Croat & L. P. Hannon, *C. mansellii* Croat & L. P. Hannon, *C. morae* Croat & L. P. Hannon, *C. munchiquensis* Croat & L. P. Hannon, *C. nambiensis* Croat & L. P. Hannon, *C. narinoensis* Croat & L. P. Hannon, *C. noramurphyae* Croat & L. P. Hannon, *C. oblongifolia* Croat & L. P. Hannon, *C. portillae* Croat & L. P. Hannon, *C. pubescens* Croat & L. P. Hannon, *C. queremalensis* Croat & L. P. Hannon, *C. risaraldensis* Croat & L. P. Hannon, *C. sagittata* Croat & L. P. Hannon, *C. sizemoreae* Croat & L. P. Hannon, *C. stellararreae* Croat & L. P. Hannon, *C. sucumbensis* Croat & L. P. Hannon, *C. timbiquensis* Croat & L. P. Hannon, *C. tokioensis* Croat & L. P. Hannon, *C. yatacuensis* Croat & L. P. Hannon, and *C. yaupiensis* Croat & L. P. Hannon. Four additional and putative new species are described in detail at the end of the taxonomic treatment and are included in the key, but not formally named; they are labeled Species 1 to 4 and are assumed to be new. They were collected as sterile plants and will be formally described only after recollection in fertile condition. Two combinations are made: *C. plowmanii* (Madison) Croat & L. P. Hannon and *C. croatiana* Grayum var. *enneaphylla* (Grayum) Croat & L. P. Hannon. Species diversity of *Chlorospatha* is greatest in the Andes of Colombia and the western Andes of northernmost Ecuador, and diminishes from northernmost Colombia into Central America and from central Ecuador southward to the border with Peru. Costa Rica has two taxa (one species, one variety), Panama four taxa (three species, one variety), Colombia 45 taxa (44 species, one variety), and Ecuador 24 species. Endemism is

¹ The authors wish to thank the curators of those institutions listed above, from which we borrowed the material used in our study, but especially Richard Wunderlin and Bruce Hansen from the University of South Florida (USF), who allowed the study of this material in their herbarium. Special thanks also go to Roy Gereau (MO) for his translations from original Latin descriptions; to Richard Keating for his contribution of the Anatomy of Vegetative Structures; to Michael Hesse and Heidi Halbritter for contributing micrographs of pollen; to Eduardo Gonçalves (Brasilia) for his contribution of information regarding *Xanthosoma*; to Michael Grayum (MO) for clarifying the concepts of shoot growth in *Chlorospatha* and providing a terminology for the various structures associated with flowering; and to Josef Bogner (M) for his translation of Engler's German text and reviewing the manuscript, also to Simon Mayo (K) for his manuscript review. We owe special thanks to the editors of *Willdenowia* for permission to use data from their journal; Elizabeth Coachman for her illustrations of the various types of styles that occur in *Chlorospatha*; Brigham Fisher (MO) for scanning of herbarium specimens for figures; and Emily Yates (MO) for figure plate layout and Carla V. Kostelac (MO) for general manuscript editing.

² This manuscript is dedicated to Lynn P. Hannon who was born on July 8, 1948, and died on July 10, 2006. Lynn's strong interest and dedication to the genus *Chlorospatha* led to this revision. Lynn spent many hours in the field with the senior author who encouraged her to write this compilation of the plants with which she became so familiar.

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highest in Colombia, with 43 species currently considered endemic, followed by Ecuador with 23 endemic species, and Central America with two endemic species.

Key words: Araceae, Central and South Americas, *Chlorospatha*.

Chlorospatha Engl. is, after *Xanthosoma* Schott, the largest genus in the tribe Caladieae Schott, in subfamily Aroideae (Mayo et al., 1997, 1998), family Araceae, with 68 species involving 69 taxa (see Appendix 1). Numerous collections of what are presumably new taxa of *Xanthosoma* were examined during the current investigation, which would eventually bring the total number of *Xanthosoma* well above the current total of 66 species (Govaerts & Frodin, 2002). This is the first complete revision of *Chlorospatha* since that of Engler and Krause (1920), although Michael Madison's generic treatment in *Selbyana* (1981) served to update the genus and was very useful for our work. *Chlorospatha* occurs from approximately 10°20'N latitude to 4°16'S latitude and inhabits a wide range of mesic habitats from near sea level to 3000 m elevation, in life zones (Holdridge, 1967) ranging from tropical moist forest to montane rainforest, with premontane wet forest the predominant ecological zone. The genus is known from dark forest understory, frequently in wet to boggy areas, in wet ravines and in association with small streams, but because of its usually small to moderate size, it is often inconspicuous. Numerous species are quite attractive, but have proved to be short-lived and demanding in cultivation, possibly owing to specialized habitat requirements. During the course of fieldwork in Colombia and Ecuador, we observed that different species did not occur together or in close proximity, although they occurred in the same general areas. Species were found only as solitary or few individual plants and occasionally in small colonies, but rarely in abundance at any given site. This would suggest the possibility that microclimates, pollination strategies, or other requirements are responsible for segregation of species. Not all species were observed in the field; therefore, it could not be said with certainty that this segregation of species is typical of the genus without further study throughout the range of the genus.

Most species are members of *Chlorospatha* sect. *Occidentales* Croat & L. P. Hannon (see Infrageneric Relationships), comprised of 40 species from Colombia and Ecuador, only two of which occur on the eastern slopes of the Andes. *Chlorospatha* sect. *Chlorospatha* is comprised of 18 taxa, most of which are from Colombia, but includes the three taxa from Central America and one species from Ecuador.

Chlorospatha sect. *Orientalis* Croat & L. P. Hannon is comprised of 10 species known only from the eastern slopes of the Andes in Ecuador.

MATERIALS AND METHODS

This revision is based on approximately 46 combined years (37 for the senior author and nine for the junior author) of field studies in Central and South America, between 1967 and 2004. All but 28 of the 72 taxa were studied in the field and/or in cultivation. Those known only from herbarium material are: *Chlorospatha amalfiensis* Croat & L. P. Hannon, *C. antioquiensis* Croat & L. P. Hannon, *C. betancurii* Croat & L. P. Hannon, *C. caldasensis* Croat & L. P. Hannon, *C. caliensis* Croat & L. P. Hannon, *C. callejasii* Croat & L. P. Hannon, *C. carchiensis* Croat & L. P. Hannon, *C. cedralensis* Croat & L. P. Hannon, *C. cogolloi* Croat & L. P. Hannon, *C. congensis* Croat & L. P. Hannon, *C. corrugata* Bogner & Madison, *C. cutucuensis* Madison, *C. gentryi* Grayum, *C. hastifolia* Bogner & L. P. Hannon, *C. jaramilloi* Croat & L. P. Hannon, *C. kressii* Grayum, *C. lehmannii* (Engl.) Madison, *C. luteynii* Croat & L. P. Hannon, *C. macphersonii* Croat & L. P. Hannon, *C. nambiensis* Croat & L. P. Hannon, *C. nicolsonii* Croat & L. P. Hannon, *C. noramurphyae* Croat & L. P. Hannon, *C. risaraldensis* Croat & L. P. Hannon, *C. stellasarrae* Croat & L. P. Hannon, *C. sucumbensis* Croat & L. P. Hannon, *C. timbiquensis* Croat & L. P. Hannon, *C. yatacuensis* Croat & L. P. Hannon, and *C. yaupiensis* Croat & L. P. Hannon. One species was published by Croat and Bogner as *Xanthosoma feuersteiniae* Croat & Bogner (Croat & Bogner, 2005) and later transferred to *Chlorospatha* by Bogner and L. P. Hannon (Bogner & Hannon, 2007). Finally, *C. hastifolia* was published in 2007 (Bogner & Hannon, 2007). Except for these, all descriptions have been prepared from both living and dried specimens. The use of "dried" preceding all or any part of the description is an indication that all that follows is based on herbarium material only. Many of the cultivated plants were based upon the living collections of Lynn Hannon from Odessa, Florida, and were disbanded upon her death.

Terminology and usage in descriptions in this revision are largely defined by Croat and Bunting (1979). Further definitions of petiole cross-sectional shapes are defined and illustrated in Croat (1983).

Ecological zones, although occasionally estimated from the first author's experience with Central and South American vegetation, are largely taken from Holdridge life zone maps (Holdridge, 1967; Holdridge et al., 1971). Holdridge life zones of areas where *Chlorospatha* occur are listed here, arranged in a generally drier to wetter order: tropical moist forest (T-mf); tropical wet forest (T-wf); tropical rainforest (T-rf); tropical moist forest transition to premontane wet forest (T-mf/P-wf); tropical rainforest transition to premontane rainforest (T-rf/P-rf); premontane moist forest (P-mf); premontane wet forest (P-wf); premontane rainforest (P-rf); premontane rainforest transition to tropical wet forest (P-rf/T-wf); lower montane moist forest (TLM-mf); lower montane wet forest (TLM-wf); lower montane rainforest (TLM-rf); montane moist forest (TM-mf); and montane rainforest (TM-rf).

Herbarium material has been widely distributed, and original field vouchers are cited for all herbaria whose material has been seen (Appendices 1, 2). Herbarium material may consist of one of three kinds: (1) complete original sets (wild collected); (2) sterile original material with an inflorescence added from a cultivated plant of the same number; (3) material collected entirely from cultivated plants. Specimens based entirely or in part on cultivated material are clearly indicated as such on the herbarium label. Herbarium specimens were borrowed from most herbaria including: AAU, B, CHOCO, COL, CUVC, DUKE, F, GH, GUAY, HUA, JAUM, K, M, MO, NY, P, PR, QAME, QAP, QCA, QCNE, S, SEL, TULV, US, and WISC.

Morphological descriptions are mostly parallel and as complete as possible. Descriptions of pistils, vitally important in the infrageneric classification of *Chlorospatha*, are particularly detailed. In order to avoid repetition, description references are made to Style Types, which are discussed and illustrated (Fig. 1) in the section Morphology of Reproductive Structures—Gynoecium.

HISTORY OF THE GENUS *CHLOROSPATHA*

The genus *Chlorospatha* was introduced by Engler in 1878, with the publication of the type, *C. kolbii* Engl., and later revised by Engler and Krause in 1920. Engler had published *Caladiopsis lehmannii* Engl. in 1905 and retained that genus as distinct from the monotypic *Chlorospatha* in the 1920 revision. After Engler's publication of *C. lehmannii*, almost 60 years would pass before Bunting's publication of *Caladiopsis dodsonii* G. S. Bunting in 1961, based on a Dodson and Thien collection made in that year. In 1978, Madison published two additional species of *Caladiopsis*, *C. atropurpurea* (Madison) Madison and

C. castula Madison, bringing the total number of *Caladiopsis* species to four. In his generic treatment, Madison (1981) recognized that there was no significant difference between *Chlorospatha* with deeply, pedately lobed leaves and *Caladiopsis* with sagittate, hastate, ovate, or ovate-cordate leaves, that character having no significance at the generic level in New World Colocasioideae (Grayum, 1986), and therefore he combined *Caladiopsis* with the older genus, *Chlorospatha*. At this time, he also assigned to *Chlorospatha* two species previously assigned to *Xanthosoma* or *Caladium* Vent.: *X. mirabile* Mast. and *C. longipodum* K. Krause. When *X. mirabile* was published in 1874, the genus *Chlorospatha* did not exist and Masters assigned the species to *Xanthosoma* with qualification, rather than describing a new genus (Masters, 1874). *Caladium longipodum* was published in 1940, based on a 1938 Schultze-Ronhof collection. *Xanthosoma mirabile* and *Caladium longipodum*, with their slender, elongated inflorescences and thin peduncles, were rightly assigned to *Chlorospatha* in Madison's treatment, as was *Caladium plowmanii* Madison (1978). With new material available from Ecuador, primarily from his fieldwork in the 1970s, Madison was able to publish three new species in his treatment of *Chlorospatha*: *C. besseae* Madison, *C. cutucuensis*, and *C. ilensis* Madison, thus bringing the total to 10 species known to science.

During the 10 years following Madison's treatment, six species and one subspecies were published: one species by Josef Bogner and Madison (*Chlorospatha corrugata* Bogner & Madison, 1985); three species and one variety by Michael Grayum (*C. croatianae* Grayum subsp. *croatiana*, *C. croatianae* var. *enneaphylla* Grayum, and *C. gentryi* in 1986; *C. kressii* in 1991); one species by Grayum and Thomas Croat (*C. hammeliana* Grayum & Croat in 1986); and one species by J. Haager and J. Jeník (*C. madisonii* Grayum & Croat in 1984). The latter species was subsequently synonymized with *C. longipoda* (K. Krause) Madison by Bogner (1985). Until 2004, a total of 16 taxa were known to science. After Madison's treatment and Grayum's publication of *C. kressii*, a large number of undetermined collections were made in Colombia and Ecuador, resulting in the publication of eight species by Croat and Lynn P. Hannon in 2004: *C. amalfiensis*, *C. antioquiensis*, *C. betancurii*, *C. callejasii*, *C. cogolloi*, *C. luteynii*, *C. macphersonii*, and *C. nicolsonii*. One species was published by Croat and Bogner as *Xanthosoma feuersteiniae* (Croat & Bogner, 2005) and later transferred to *Chlorospatha* by Bogner and L. P. Hannon (Bogner & Hannon, 2007). Finally, *C. hastifolia* was published in 2007 (Bogner & Hannon,

2007). As predicted by Grayum (1986), the dramatic increase in the number of collections has resulted in the discovery of many new species.

COLLECTING HISTORY

The earliest collections of *Chlorospatha* date from the late 19th century, during the heyday of European collecting in the Neotropics, the first two resulting in the publication of the Colombian species *C. kolbii* in 1878 collected by Gustav Wallis, and *C. mirabilis* (Mast.) Madison (as *Xanthosoma mirabile* Mast.) in 1874, collected by Benedict Roezl. Carl B. Lehmann made six collections between about 1900 and 1906, two being *C. lehmannii* (Engl.) Madison (\equiv *Caladiopsis lehmannii* Engl.) and four that remained undescribed until the present work: *C. caliensis* Croat & L. P. Hannon, *C. congensis* Croat & L. P. Hannon, *C. grayumii* Croat & L. P. Hannon, and *C. timbiquensis* Croat & L. P. Hannon. Incredibly, only 11 collections of *Chlorospatha* were made by 11 collectors between 1906 and 1970. In 1913, G. Forget collected *C. mirabilis*. Tracy E. Hazen made the first collection of *C. bullata* Croat & L. P. Hannon in 1922, described here. *Chlorospatha croatiana* was first collected by Paul C. Standley in 1924 and later by Harley Harris Bartlett in 1940. In 1933, Alexander E. Lawrance was the first collector of what would later become the type for *C. croatiana* var. *enneaphylla*. Arnold and Hertha Schultze-Ronhof made the first collection of *C. longipoda* (K. Krause) Madison (\equiv *Caladium longipodum* K. Krause) in 1938, which would later serve as the type. Erik Asplund also collected this species in 1956. Elsworth P. Killip collected the type for *C. grayumii* in 1939, a species new to science. Julian A. Steyermark was the first to collect *C. ilensis*, in 1943. Callaway Dodson made the first collection of *C. dodsonii* (G. S. Bunting) Madison in 1961, which also served as the type. In 1958, Jesus Idrobo made the first collection of *C. huilensis* Croat & L. P. Hannon, a species new to science. Of these collectors, only Dodson made additional collections of *Chlorospatha* after 1970. There are several possible reasons why *Chlorospatha* has been infrequently collected until recently, the first being its small to moderate size and, except in the case of maculate or colorful species, its usually inconspicuous coloration and markings. It is usually found only in undisturbed forest and often overlooked on the forest floor, perhaps mistaken for immature plants of larger growing species of *Xanthosoma*, particularly when found in the sterile state. Collections of *C. croatiana*, the largest species in the genus, were misfiled for many years as *Xanthosoma* (Grayum, 1986). In fact, there are presently far more collections of this species and its related taxon

(55) than of any other *Chlorospatha*, perhaps because it is more conspicuous, owing to its larger size. The lack of roads into the wet areas where *Chlorospatha* occurs would certainly have been a limiting factor then, which is true even today, although more roads exist now.

Sixty-six collections of *Chlorospatha* were made in the 1970s, thus marking the beginning of a dramatic increase in collections, ultimately leading to Michael Madison's treatment of the genus in 1981. Most of these collections were made by Madison or Thomas B. Croat. Eleven of the 15 Croat collections made prior to 1980 were of Central American taxa that would not be recognized as *Chlorospatha* until the publication of *C. croatiana* by Grayum and *C. hammeliana* by Grayum and Croat in 1986, with a 1973 Croat collection serving as the type for *C. croatiana*. The remaining four Croat collections represent four species, three of which are new to science, *C. bullata* and *C. morae* Croat & L. P. Hannon from Colombia, and *C. pubescens* Croat & L. P. Hannon from Ecuador. Croat was also the first to collect *C. morae*. All of Madison's 28 collections of *Chlorospatha* were made in Ecuador between 1970 and 1981, except one collection of *C. croatiana* made in Panama. Madison was the first to collect specimens that served as the types for three species: *C. besseae*, *C. castula* (Madison) Madison, and *C. cutucuensis*. Additionally, his collections were the first made of four species and one combination new to science, *C. carchiensis* Croat & L. P. Hannon, *C. hastata* Croat & L. P. Hannon, *C. litensis* Croat & L. P. Hannon, *C. plowmanii* (Madison) Croat & L. P. Hannon (\equiv *Caladium plowmanii*), and *C. yaupiensis* Croat & L. P. Hannon, with his collections serving as the types for *C. carchiensis* and *C. yaupiensis*. Madison also collected *C. atropurpurea*, *C. dodsonii*, and *C. longipoda*, but made no additional collections of *Chlorospatha* after his treatment of the genus in 1981.

Other than Croat and Madison, only 12 individuals made collections in the 1970s, Callaway Dodson being the most prolific, having made seven collections in western Ecuador, two of which served as the types for *Chlorospatha atropurpurea* and *C. ilensis*. Dodson made only a few more collections in the 1980s, one being the first collection of a species new to science, *C. longiloba* Croat & L. P. Hannon, after which he made no additional collections of *Chlorospatha*. The combined collections of seven of the remaining collectors, Robert Dressler, James Folsom, Barry Hammel, James Luteyn, Paul Maas, John Shepherd, and Djaja Djendoel Soejarto represent 10 collections of *C. croatiana* in Panama and three

collections of a new combination, *C. croatiana* var. *enneaphylla* (Grayum) Croat & L. P. Hannon, in Colombia and Panama. Isidoro Cabrera made a collection in southern Colombia that later served as the type of *C. hastifolia*. Alwyn Gentry made three collections, two of which were the first collections of, and served as the types for, *C. gentryi* and *C. nicolsonii*. James Luteyn was the first to collect *C. antioquiensis*, with his collection serving as the type. Bernt Løjtnant made the only collection of *C. sucumbensis*, which serves as the type for this new species. Timothy Plowman collected the type for *C. plowmanii*. Olga de Benavides made one collection of what is possibly *C. ricaurtensis* Croat & L. P. Hannon, a new species from Colombia. Only de Benavides, Gentry, Hammel, Luteyn, and Plowman went on to make additional collections after 1979, during which time Gentry made only four collections, two of which are new. His was the first collection of *C. bogneri* Croat & L. P. Hannon and the only collection of *C. yatacuensis*, which serves as the type. Luteyn made the first collections of *C. luteynii*, *C. tokioensis* Croat & L. P. Hannon, and the only collection of *C. stellarreae*, with the collections serving as the types for these species, the last two being new to science, and also collected the type for *C. cogolloi*, a species new to science, and the type for *C. macphersonii*. Hammel made several collections in Panama and Colombia, one of which remains the only fertile collection of and served as the type for *C. hammeliana*. Two collections were made by de Benavides, one of which serves as the type for *C. planadensis* Croat & L. P. Hannon, a species new to science. Plowman made two collections, one of which is new to science, *C. pubescens*.

Prior to 1980, less than 100 collections of *Chlorospatha* had been made, most of these in Ecuador (44) or Central America (24), with only 22 collections having been made in Colombia. Subsequently, numerous collections were made in Ecuador, and it was not until after 1979 that considerable numbers of collections were made in Colombia (119 collections), 45 of which were made by the senior author, Thomas Croat, who also made 84 collections in Ecuador and 17 in Central America during this period. Of the 383 total collections of *Chlorospatha* included in the present treatment, approximately 41% (161) were made by Croat. After 1979, Croat collected extensively in Colombia, Ecuador, and Central America, alone or in conjunction with one or more collectors, and made 146 collections representing 42 species and one taxon, of which 35 species are new to science. Of these 35 species, Croat made the only collections of *C. bayae* Croat & L. P. Hannon, *C.*

chocoensis Croat & L. P. Hannon, *C. engleri* Croat & L. P. Hannon, *C. hannoniae* Croat, *C. limonensis* Croat & L. P. Hannon, *C. munchiquensis* Croat & L. P. Hannon, *C. queremalensis* Croat & L. P. Hannon, *C. ricaurtensis* Croat & L. P. Hannon, and *C. sagittata* Croat & L. P. Hannon, with these collections serving as the types for these species. Croat was also the first to collect *C. boosii* Croat & L. P. Hannon, *C. maculata* Croat & L. P. Hannon, *C. oblongifolia* Croat & L. P. Hannon, and *C. portillae* Croat & L. P. Hannon, with these collections serving as the types. Croat's collections served as the types for five additional new species: *C. hastata*, *C. huilensis*, *C. litensis*, *C. longiloba*, and *C. pubescens*. Since 1979, Croat has also collected *C. bogneri*, *C. bullata*, *C. giraldoi* Croat & L. P. Hannon, *C. jaramilloi*, *C. mansellii* Croat & L. P. Hannon, *C. nambiensis*, *C. nicolsonii*, *C. noramurphyae*, *C. planadensis*, *C. plowmanii*, and Species 1–3, all of which are new to science except *C. nicolsonii*.

Fifty-nine collectors made collections of *Chlorospatha* between 1980 and 2004. Of those not previously mentioned, 22 worked exclusively in Colombia, 25 only in Ecuador, and only four exclusively in Central America. The most noteworthy collections from this period, other than those previously mentioned, were made by 12 of these collectors and include either the types or first collections of species new to science. Ricardo Callejas made nine collections in Colombia, representing three species: *C. antioquiensis*, *C. luteynii*, and the only collection of *C. callejasii* Croat & L. P. Hannon, which serves as the type. Michael Grayum made two collections of *C. croatiana* in Costa Rica, two collections in Ecuador of previously published species, and four collections in Colombia including the only collection of *C. kressii*, which served as the type, and three species new to science, *C. grayumii*, *C. maculata*, and *C. morae*. Alvaro Cogollo and John Pipoly each made five collections in Colombia, with Cogollo making the first collection of *C. cogolloi*, Pipoly, the type collection of that species, and both making collections of *C. nicolsonii*. Pipoly also collected *C. dodsonii* in Ecuador. Jaime Jaramillo also made five collections, all in Ecuador, two of which proved to be new, including the first collection of *C. jaramilloi*, which serves as the type, and a collection of *C. plowmanii*. The two Colombian collections of Jorge Giraldo serve as the types for two new species, *C. bullata* and *C. giraldoi*. Lynn Hannon made five collections in Ecuador, including *C. pubescens* and the type for *C. mansellii*, both of which are new. Julio Betancur made four collections, all in Colombia, including two species new to science, *C. narinoensis* Croat & L. P. Hannon, and the first collection of *C. risaraldensis*, which serves as the type, and the type for

C. betancurii Croat & L. P. Hannon. Honora Murphy and Gustavo Lozano each made one collection, each representing a species new to science, with the Murphy collection being the only collection of *C. noramurphyae* Croat & L. P. Hannon, which serves as the type, and the Lozano collection serving as the type for *C. morae*, the only fertile collection of that species. Mary Sizemore made the first and only collection of *C. sizemoreae* Croat & L. P. Hannon, which serves as the type. Jens Bittner collected the type of *C. bogneri*, a species new to science.

Each of 13 collectors made one to several collections of species new to science during this period, but these were neither the types nor the first collections of these species. Carlos Cerón, Ralf Leimbeck, Walter Palacios, and Patricio Yáñez collected *Chlorospatha plowmanii*, with Palacios also collecting *C. pubescens*, both Ecuadorian species, as did Ray Baker and Libby Besse. Cerón also collected *C. longipoda*. Four collections of two new species were made in Colombia by Pilar Franco, *C. litensis* and *C. nambiensis*. Both of Carla Restrepo's collections represent species new to science, *C. bogneri* and *C. planadensis*. The remaining collections were single collections made by Anders Barfod of *C. litensis*, J. L. Fernández-Alonso of *C. risaraldensis*, Jorge Ramos of Species 4, Daniel Rubio of *C. hastata*, and William Vargas of *C. giraldoi*, all species new to science.

The remaining 27 of the 59 collectors who were active during this period made one to several collections of previously published species or sterile specimens that could not be determined with certainty. These collectors are: Hugh W. Churchill, John Clark, Xavier Cornejo, Hermes Cuadros, Thomas Delinks, Linda Albert de Escobar, Romiro Fonnegra, Thassilo Franke, Alcira Gomez, George Haager, Gunnar Harling, Sandra Knapp, Marcela Mora, Felipe Cardona Naraño, Nigel Pitman, Axel Dalberg Poulsen, Carlos Quelal, Juan José Ramírez, Orlando Rangel, Jimena Rodríguez, Sari Roponen, Elaine Spear, Bertil Ståhl, Kenneth Sytsma, Sue Thompson, Galo Tipaz, and Milton Tirado.

These recent collections have provided additional specimens of both published species and previously unknown species, thus affording a richer and much broader view of the variation of species within local populations and across their known range. A better grasp of the distribution of individual species is now available as well. This is mainly due to the large number of collections made by more collectors during the last 20 years, particularly in Colombia, which was previously poorly represented. It is hoped that the increase in the number of collectors and collections continues to accelerate.

FOSSIL HISTORY

There are, as yet, no reports of fossil *Chlorospatha* in the literature.

INTERGENERIC RELATIONSHIPS

The last thorough taxonomic revision of the Araceae was that by Engler (1905–1920), conducted partly in collaboration with Krause (Engler & Krause, 1920). The final revision included eight subfamilies of Araceae, with *Chlorospatha* in the subfamily Colocasioideae, tribe Colocasieae, and subtribe Caladiinae. Colocasieae shared the subfamily with two other tribes, Syngonieae and Ariopsidae. The subtribe Caladiinae was one of five subtribes, the others being Steudnerinae, Hapalininae, Colocasiinae, and Alocasiinae. Subtribe Caladiinae was comprised of *Aphyllarum* S. Moore, *Caladiopsis* Engl., *Caladium*, *Chlorospatha*, and *Xanthosoma*. Bogner and Nicolson (1991) retained Engler's subfamily Colocasioideae, but eliminated the subtribe, thus raising subtribe Caladiinae to tribal status as Caladieae, which included *Chlorospatha*, *Xanthosoma*, *Caladium*, *Scaphispatha* Brongn. ex Schott, and *Jasarum* G. S. Bunting, with *Aphyllarum* placed in synonymy with *Caladium*. Grayum (1990) also retained the subfamily Colocasioideae and placed *Chlorospatha* in the tribe Caladieae, but retained subtribe Caladiinae, comprised of *Chlorospatha*, *Caladium*, *Xanthosoma*, and *Aphyllarum*, choosing to retain *Aphyllarum*. A comparison of the major systems of classification at the suprageneric level was made by Croat (1990) and included the systems of Hotta (1970), Grayum (1990), and Bogner and Nicolson (1991). In an attempt to bridge differences in the systems of Bogner and Nicolson, Grayum, and Hay and Mabberley (1991), Mayo et al. (1995) conducted a sweeping survey and produced a cladistic analysis that maintained essentially the same alliances suggested by Grayum (1990), but placed all araceous genera with unisexual flowers in subfamily Aroideae. Keating (2003) sank Colocasioideae into Aroideae, but had two other unisexual subfamilies, Philodendroideae and Schismatoglottiidae. The systems of classification of Mayo et al. (1995) and Keating (2003) have taken into account all evidence to date, including the extensive molecular studies of French et al. (1995). In the most recent revision (Mayo et al., 1997), *Chlorospatha* was placed in tribe Caladieae: *Scaphispatha*, *Caladium*, *Jasarum*, *Xanthosoma*, *Chlorospatha*, *Syngonium* Schott, and *Hapaline* Schott.

The genus of Araceae most easily confused with *Chlorospatha* is *Xanthosoma*, which is closely

related, both having pollen shed in permanent tetrads (Madison, 1981; Grayum, 1984; Bogner, 1997) and a modified style, unlike the other genera within the subfamily Colocasioideae (Mayo & Bogner, 1988). However, the pollination biology is distinct in each, resulting in differences in floral and inflorescence characters. Mayo and Bogner (1988) suggested the possibility of pollen tetrads and a modified style as synapomorphies that would support an infratribal group comprised of *Chlorospatha* and *Xanthosoma*. The genera are palynologically distinct, the individual grains and tetrads of *Chlorospatha* pollen being, on average, more than 50% smaller than those of *Xanthosoma* (Grayum, 1984), basically binucleate and starchless, whereas the pollen of *Xanthosoma* is frequently trinucleate and always starchy (Grayum, 1985, 1986).

The differences between the genera were apparent even in the first two collections of *Chlorospatha*. Masters, obviously somewhat aware of the differences, published *Xanthosoma mirabile* in 1874, with reservations about the generic designation, and Madison (1981) later rightly assigned the species to *Chlorospatha*. Engler (1878) recognized the genus *Chlorospatha* as distinct from *Xanthosoma* in his publication of the type species, *C. kolbii*. At that time, taxa of *Xanthosoma* with cormose and caulescent stems were not considered distinct and were combined, without sectional distinction, in the genus *Xanthosoma*. Engler initially believed that the collection of what would be *C. kolbii* was possibly *X. helleborifolium* (Jacq.) Schott, a cormose species in what is now *Xanthosoma* sect. *Acontias* (Schott) Engl. Therefore, when the collection of *C. kolbii* flowered, he distinguished *Chlorospatha* from *Xanthosoma* only on the basis of floral characters, only one of which can now be maintained without qualification, that being the clear demarcation of the spathe tube and blade by a prominent constriction at and toward the apex of the tube in *Xanthosoma*. The inflorescence of *Chlorospatha* is small and delicate compared to the usually larger and more robust inflorescences of *Xanthosoma* in plants of comparable size, with the spathe weakly or not at all constricted between the tube and blade. In *Chlorospatha*, the spathe tube is narrow and elongated, less than 1.5 cm in diameter (pre-anthesis), even in the largest inflorescences, and usually 5 to 9 times longer than wide. The spathe tube in *Xanthosoma* is usually somewhat globose and is more than 1.5 cm in diameter, even in small inflorescences, and usually less than 2 times longer than wide. These differences would indicate the involvement of different pollinators. *Xanthosoma* is pollinated by euglossine bees, beetles of Nitidulidae

and Scarabaeidae (Mayo et al., 1997), and possibly other beetles. *Chlorospatha* is pollinated by beetles of Staphylinidae (Mayo et al., 1997), possibly by flies and other small beetles, these having been collected in the inflorescences (Madison, 1981). According to Madison (1981), beetles fly to the inflorescence of *Xanthosoma* at dusk, where they are trapped and remain in the spathe tube until the following evening, thus exhibiting a nocturnal pollination syndrome. In *Chlorospatha*, female anthesis occurs during the middle of the day, thus indicating a diurnal pollination syndrome (see Pollination Biology below). The more or less globose spathe tube of *Xanthosoma* (section *Xanthosoma*) opens broadly (laterally) at the apex at anthesis, allowing entry of the pollinators. Recent observations of 19 taxa of *Chlorospatha* in cultivation, and photographs of two additional species, revealed that in 11 of these, the entire spathe opened narrowly or broadly most of its length, with the margins of the tube directed forward or outward, a condition not observed in *Xanthosoma* sect. *Xanthosoma*. Observations in the field corroborated the existence of this condition in seven of these taxa (one from a photograph), and since the condition occurs across the known geographical range of the genus and in vegetatively and floristically diverse taxa, it would be expected to occur in other, perhaps numerous taxa. This condition would suggest a greater range in the size of possible pollinators than was previously assumed. Unfortunately, it is not possible to determine this condition in dried material.

Engler (1879) did not consider vegetative characters in his treatment, thereby implying that the two genera were indistinguishable in the sterile state, which is true only in some cases. Taxa with caulescent stems, in both genera, can appear to be acaulescent when initiating growth from bulbils, at or below the soil surface, or when the stem is epigaeous and obscured by detritus. However, *Chlorospatha* is never cormose and its invariably caulescent stem makes it easily distinguishable from the strictly cormose taxa in *Xanthosoma* sect. *Acontias*. Therefore, *Xanthosoma* sect. *Xanthosoma* is henceforth referred to simply as “*Xanthosoma*”; members of *Xanthosoma* sect. *Acontias* have no relevance in this discussion. In the sterile state, *Chlorospatha* is, in most respects, indistinguishable from the strictly caulescent taxa of *Xanthosoma*, in plants of comparable size. Taxa of *Chlorospatha* are usually of relatively small to moderate stature, usually less than 1 m tall, with the stem not exceeding 4 cm in diameter. Most mature taxa of *Xanthosoma* are large, arborescent plants that could not be confused with *Chlorospatha*, except perhaps in juvenile or less-

than-mature states. The diameter of the stems of these large *Xanthosoma* usually far exceeds the maximum observed in *Chlorospatha*.

The caulescent taxa of the two genera share the same broad range of leaf blade shapes, which can be entire, simple and ovate, sagittate, hastate, deeply lobed, or compound with no notable differences in venation. Although there are some distinguishing features in the vegetative characters of the two genera and an unquantifiable delicacy and form to the vegetative aspects of most *Chlorospatha*, which are apparent to the authors, it is still usually entirely on the basis of fertile characters that the two genera can be distinguished with certainty, as Engler maintained.

Engler maintained that the spadix of *Xanthosoma* differed from that of *Chlorospatha* in having the female and sterile male flowers densely arranged (the fertile male flowers are densely arranged in both genera). He further implied that the sterile staminate portion of the spadix in *Xanthosoma* is comparatively short. Some of these differences clearly apply in the case of *C. kolbii*, in which the sterile portion of the spadix is long, relative to the lengths of the other two portions, and the pistils and sterile male flowers are laxly arranged; however, these character states do not pertain throughout *Chlorospatha*. As currently understood, the fertile staminate portion of the spadix in *Xanthosoma* is usually long, relative to the lengths of the other portions, with the sterile flowers densely arranged, as Engler maintained. In *Chlorospatha*, this portion can be either long, as in most *Xanthosoma*, or much shorter than any observed in that genus, occasionally comprising only a small fraction of the total length of the spadix. Sterile flowers can be either laxly or densely arranged in *Chlorospatha*, but are more laxly arranged than in *Xanthosoma* in most taxa, with those of *C. kolbii* representing an extreme but not unique condition in the genus. Engler maintained that the sterile flowers of *Xanthosoma* differed from those of *Chlorospatha* in always being morphologically similar to the synandria and presumably prismatic (as viewed from above). Sterile flowers of *Chlorospatha* can also be prismatic, though in only a few taxa, as well as subprismatic in numerous taxa, or irregularly lobed, fungiform, or prominently branched (see Sterile Flowers). However, even when the fertile portion of the spadix is relatively long and the sterile flowers prismatic or subprismatic in *Chlorospatha*, it is easily distinguishable from *Xanthosoma*, because the sterile portion is more or less cylindrical, with the flowers comparatively weakly elongated in the direction of the axis (or not at all). In *Xanthosoma*, this portion is usually more or less attenuated toward

the apex, with the associated flowers prominently elongated in the direction of the axis and the basal flowers conspicuously wider and thicker, appearing swollen.

The spadix of *Xanthosoma* is more robust, with the pistillate portion usually shorter than either the sterile or fertile staminate portions, frequently markedly so, and usually adnate to the spathe only at the base or not at all. The spadix of *Chlorospatha* is delicate and narrow, with the pistillate portion longer than the sterile portion (not always in *C. atropurpurea*), occasionally longer than the fertile staminate portion, and in part or entirely adnate to the spathe. Only in a few species of *Chlorospatha* is the spadix adnate only narrowly at the base or only along the stipe (when present). The pistillate portion of the spadix of *Chlorospatha* is narrow and comparatively laxly flowered, with no more than six flowers across the axis (as viewed from above) and usually only three to four. The pistillate portion in *Xanthosoma* is comparatively broad and densely flowered, with no fewer than seven flowers across the axis, usually many more. The pistils are so densely arranged in *Xanthosoma* that they are prismatic in appearance (this probably only a matter of crowding), a condition that does not typically occur in *Chlorospatha* and is diagnostic on the generic level, being directly related to morphological differences in the ovaries and stylar regions of the two genera. One collection of *C. mirabilis* (Croat & Mora 83686) is the only exception. In that collection, the pistils in the central three fourths of the pistillate portion of the spadix appear to be prismatic, most ovaries being coherent most of their lengths; however, the styles are morphologically distinct from those of *Xanthosoma* and not at all coherent with adjacent styles.

Engler described the ovaries of *Xanthosoma* as ovoid or cylindrical and the styles as disklike and connate at the margins, as opposed to the subglobose or cylindrical ovaries of *Chlorospatha kolbii*, which also has somewhat disklike styles, but with the margins neither connate nor coherent. Ovoid and cylindrical ovaries occur also in *Chlorospatha*, as well as subglobose and obtusely conical or obconical ovaries, and although these can be more densely arranged than in *C. kolbii*, they are as densely arranged as in *Xanthosoma* in only one collection of *C. mirabilis* (see above). In *Xanthosoma*, the sides of the ovaries are entirely coherent. The styles in *Xanthosoma* are not connate (fused) as Engler maintained, although they appear to be so, but are coherent (J. Bogner, pers. comm.), as are some styles in some *Chlorospatha*. Typically, the ovaries and, therefore, the pistils, appear separate and distinct in

Chlorospatha, the sides of the ovaries being either free or coherent only at some points along the sides, i.e., weakly coherent. Similarly, the margins of the styles of *Chlorospatha* are usually either free, weakly coherent or coherent on some styles and otherwise free or weakly coherent on the remaining styles (on a single spadix).

The morphology of the style in *Chlorospatha* easily serves to separate it from *Xanthosoma*, regardless of the size of the plant. Mayo and Bogner (1988) rightly maintained that the two genera were distinctive in having modified (thickened) styles. Although the style is clearly modified in all *Chlorospatha*, the style in all species, except 11 of the 12 species from the eastern slopes of the Andes in Ecuador, could not be considered analogous to that of *Xanthosoma*. In view of the diversity of styler morphology exhibited within *Chlorospatha*, its disparity in *Chlorospatha* and *Xanthosoma* and the currently limited knowledge of the complexities of this morphology, it would seem best to apply the terminology of Mayo et al. (1997), wherein the style is referred to as the “styler region,” in recognition of the fact that a “style” is, by definition, attenuated, a condition which clearly does not apply in *Xanthosoma* or all *Chlorospatha*. The styler region in *Xanthosoma* is prominently thickened and tough (Madison, 1981; Mayo & Bogner, 1988), usually the same diameter as or slightly broader than the ovary (Mayo & Bogner, 1988; Mayo et al., 1995, 1997), with the styles and ovaries more or less coherent with those of adjacent flowers. The styler region of *Chlorospatha* is usually expanded into a thin, fragile, spreading mantle that is, for the most part, free from the ovary and is frequently broader than the ovary apex, occasionally as much as 3 times broader. In some *Chlorospatha*, the mantle is disklike, usually somewhat thicker but equally fragile and approximately as wide as or narrower than the ovary apex. Neither the apex nor sides of the ovary are completely coherent with those of adjacent ovaries in *Chlorospatha* except in some flowers of one collection of *C. mirabilis* (Croat & Mora 83686). In the 11 eastern Ecuadorian species mentioned above, the style is not expanded into a mantle, but is exceedingly thin and not coherent with adjacent styles. More than half of *Chlorospatha* species have the style more or less attenuated, thus elevating the stigma, a condition not observed in *Xanthosoma*, in which the stigma is sessile.

Engler (1879) maintained that axile placentation in *Xanthosoma* also distinguished that genus from *Chlorospatha*, the placentation in *C. kolbii* being subaxile. As presently circumscribed, placentation in *Chlorospatha* can be axile, subaxile, pseudoaxile, sub-

basal, or basal. The ovules per locule in *Chlorospatha* with plurilocular ovaries are usually few, (three)four to 10(to 12), with three species occasionally having as many as 14, and two species which rarely have as many as 15 to 16(to 20) in unilocular ovaries. The ovaries of *Xanthosoma* have (12 to)20 to very numerous ovules per locule (Mayo et al., 1997).

The peduncle of *Xanthosoma* is usually comparatively short, occasionally long, usually more than 5 mm in diameter and is not held within the petiole sheath its entire length. The peduncles of *Chlorospatha* are usually long, occasionally longer than the petioles, or much shorter, and always exceedingly slender, usually less than 4 mm in diameter, and only to 5(–6) mm in diameter in a few more robust taxa with both long peduncles and petioles. The entire length of the peduncle is usually held within the petiole sheath, thus giving the inflorescence an erect habit despite the slender peduncle; rarely is it held only weakly within the sheath toward the base, e.g., *C. hammeliana*.

The infructescence of *Chlorospatha* is elongated, usually much longer than broad, with a maximum diameter of 1.5 cm (on drying). The infructescence of *C. corrugata* had the least elongated of those examined, and was 3.5 times longer than wide, the infructescence typically being 4 to 10 times longer than wide in *Chlorospatha*. The infructescence of *Xanthosoma* is usually subglobose to globose and even when somewhat elongated, it is usually less than 2 times longer than wide. As would be expected, considering the small number of pistils visible across the axis of the spadix in *Chlorospatha*, there are few berries across the axis and comparatively more in *Xanthosoma*, with the berries depressed-globose and somewhat flattened apically in *Chlorospatha* and more or less cylindrical and more elongated in *Xanthosoma*.

MORPHOLOGY OF VEGETATIVE STRUCTURES

ANATOMY

Vegetative anatomy. (Contributed by R. C. Keating; vouchers cited by Keating, 2003).

Leaf surface. Cuticle smooth on both surfaces. Epidermis cells polygonal with straight anticlinal walls on both surfaces (1–2:1 length-to-width ratio). Stomata abaxial and brachyparacytic. Subsidiary cells broad or narrow, rounded or angular. Venation: midrib and basal lobe primaries arising from summit of petiole. Midrib prominent, secondary veins acute or narrowly acute, curved and apically ascending, widely spaced or irregular. Tertiary veins variable, sometimes parallel with secondary veins or reticulate.

Higher orders reticulate and merging marginally at more or less straightened collective vein.

Leaf cross-section. Structure dorsiventral. Cuticle thin. Epidermis with adaxial cells large, rounded; abaxial cells small to large, variably shaped, occasionally papillate. Stomata level with surface. Mesophyll with two columnar palisade layers (4–6:1 length-to-width ratio), forming 25% of mesophyll area; spongy zone of ca. five layers of irregularly shaped, short-armed cells forming an aerenchyma of large, rounded, usually substomatal air cavities, some aerenchyma cells with 1-seriate partitions, one partition cell between corner cells. Air cavities forming about 80%–90% of spongy layers. Collenchyma as small strands subtending peripheral bundles.

Vascular bundles. In midrib, ca. 12 around abaxial periphery and ca. eight scattered in center; bundles not large or well-differentiated; xylem with one protoxylem cell with one metaxylem cell occasionally present phloem as a circular strand. Laticifers one or two anastomosing tubes lateral to each vascular bundle; branches may penetrate palisade tissue, ending at epidermis. Tannin cells with dark contents common in palisade layer. Crystals as raphides rare in single bundles in narrow, rounded ended, thin-walled bifurcate idioblasts oriented across aerenchyma partitions, or in rounded cells and uncommon: raphides subepidermal in midrib; druses large, very common in mid-mesophyll, often bordering large vascular bundles; small druses common in palisade cells; crystal sand in abaxial guard cells of stomata.

Petiole cross-section. Cuticle thin and striate. Epidermis cells large and rounded. Collenchyma as peripheral rounded strands, ca. 12 layers deep, one to three layers beneath epidermis. Chlorenchyma: chloroplasts sparse in outer six to eight layers of ground tissue, ground tissue cells mostly compact. Vascular bundles scattered, two sizes, largest mixed with very small bundles comprised almost entirely of phloem. Sclerenchyma: fibers in one to three layers capping phloem in one specimen of *Chlorospatha plowmanii* (= *Caladium plowmanii*) (in Keating 2003, this specimen, *Plowman et al.* 3979, was cited as *Chlorospatha longipoda*). Laticifers anastomosing, two to three lateral to vascular bundles and ramifying throughout ground tissue. Tannin cells occasional in ground tissue. Starch granules occasional in outer ground tissue. Crystals: druses common in compact ground tissue and at margins of air cavities.

Habit and growth patterns. Growth is continuous throughout the year in *Chlorospatha*. In the absence of any known observations of growth over time in *Chlorospatha* in habitat, a few observations made of plants in cultivation will be presented here. In cultivation (at ca. 28°N, ca. 20 m elevation), plants were maintained between 60°F/15.5°C and 86°F (90°F)/30°C (32.2°C), well within the minimum temperature range, but possibly exceeding the maximum temperature found in habitat. During the months of November through March (approximately), vegetative growth either slowed in varying degrees or in some cases appeared to stop. Of the species with reduced growth rate, some continued to flower and others not at all, but with each species flowering (or not) in accordance with its known schedule in habitat. The reduced rate of growth is possibly due to the reduced light intensity and shortened day length at this latitude.

Growth patterns for *Xanthosoma* were diagrammed schematically by Engler (1877) and Ray (1988). There is no information available pertaining to shoot growth in *Chlorospatha*. Ray did not consider *Chlorospatha* in his survey of shoot organization (1988) or treatment of diversity of shoot organization (1987b), nor did Grayum (1990) in his later review of shoot growth. However, Ray made observations regarding *X. violaceum* Schott, in *Xanthosoma* sect. *Xanthosoma*, which would probably apply to *Chlorospatha*, the vegetative aspects of *Xanthosoma* sect. *Xanthosoma* and *Chlorospatha* being the same in most respects. A brief summary of their observations is provided here, and the reader is referred to Grayum (1990) and Ray (1987a, 1987b, 1988) for more detailed accounts. The terminology used here is that of Ray (1987a). Growth of the main axis is monopodial in all Araceae, at least until the time of first actual or aborted flowering, after which the mature stem of *Xanthosoma* has polyphyllous sympodial growth, wherein the stem articles bear a variable number of leaves, whether foliage leaves or cataphylls, before terminating in a sympodial leaf subtending an inflorescence bud which may or may not develop and mature to anthesis. A stem article is a section of the stem produced from a single meristem, from its inception to its termination in a developed or aborted inflorescence (Grayum, 1990). The main axis of the stem consists of a series of such articles, with flowering morphologically terminal, although it appears to be axillary. Although the stem appears to be unbranched, it actually produces a new branch following each sympodial leaf. In *X. violaceum*, growth of the new branch is sylleptic, meaning that the vegetative bud does not rest relative to the

parent shoot. The first leaf of the new growth (of an article) is a sylleptic prophyll. In *Xanthosoma* sect. *Xanthosoma* and presumably *Chlorospatha*, the sylleptic prophyll is a cataphyll.

The growth habit of *Chlorospatha* is terrestrial or occasionally hemiepiphytic or emergent aquatic. Most taxa are consistently terrestrial. Only two species have been reported as exclusively epiphytic, *C. risaraldensis* and *C. yatacuensis*. Both collections of *C. risaraldensis* were reported as “climbers.” *Chlorospatha yatacuensis* is known only from the type and is reported as “epiphytic on tree stump.” It is likely that both species are usually terrestrial. Eleven taxa are reported as both terrestrial and epiphytic: *C. antioquiensis*, *C. cogolloi*, *C. dodsonii*, *C. croatian* var. *enneaphylla*, *C. giraldoi*, *C. grayumii*, *C. ilensis*, *C. longiloba*, *C. longipoda*, *C. nicolsonii*, and *C. planadensis*. One or more collections of each of these taxa were reported as either “epiphytic” or “epiphytic or terrestrial,” with two collections of *C. longiloba* reported respectively as a “liana” or “hemiepiphyte.” The report of *C. longiloba* occurring as a liana can be excluded, lianas being woody-stemmed vines of the forest canopy, whereas the stem of *Chlorospatha* is always somewhat fleshy. The type of *C. dodsonii* was collected as an “epiphyte on tree trunk.” Labels of herbarium collections that report the habit as “epiphytic” are often suspect, when in fact, the collections were probably rooted in the soil and therefore, were technically hemiepiphytic. This was the condition observed (by the authors) in *Chlorospatha*; therefore, these collections would be secondary hemiepiphytes (Putz & Holbrook, 1986), having the stems growing and rooted in or on the soil. The condition occurs in species of *Chlorospatha* that grow erect and in those with the stem decumbent and erect at the apex, although it is reported in only three species that can be erect-growing: *C. dodsonii*, *C. grayumii*, and *C. ilensis*. All erect-growing species frequently produce adventitious roots on the exposed portion of the stem and should the roots come in contact with a tree or possibly a rock, it is likely that these would attach themselves, particularly in the presence of mosses. The fact that the condition occurs in both erect-growing and decumbent species combined with field observations (by the authors) of different populations of two species, *C. longiloba* and *C. longipoda*, suggest that the condition is probably adventitious rather than innate. *Chlorospatha longipoda* was found almost exclusively as a decumbent-growing terrestrial, but when the growing stem encountered an obstacle such as a tree trunk, it would occasionally become appressed to the trunk, with the appressed portion no more than 10 cm long.

On several occasions, *C. longiloba*, also with a decumbent habit, was observed with the appressed portion as much as 1–4 m long, with the stem still retaining its attachment to the ground. In two instances, the elongate stems were loosely held within thick mats of moss among the long thorns of palms and not attached to the trunks. Plants were also found attached to moss-covered tree trunks. There was no apparent difference between the roots observed in the soil and those attached to the trees, and those attached to the trees did not grow downward toward the soil surface. The plants were easily removed, the roots being thin and fragile, as is typical of *Chlorospatha*, and their attachment tenuous, thus differing significantly from the roots of true hemiepiphytes in Araceae. However, it would not be surprising to find other species, perhaps many, at least occasionally assuming this habit, provided that the roots received the moisture necessary to sustain them. Since *Chlorospatha* is known only from consistently mesic habitats, this would not be unlikely, especially considering that almost 20% of known taxa have been reported as at least occasionally hemiepiphytic. Although collections are occasionally made in bright light in disturbed areas, this situation is unnatural, *Chlorospatha* being a plant of the dark forest understory, not requiring the brighter light of an exposed position to achieve maturity and flowering. An elevated position, as a hemiepiphyte, would therefore, provide no apparent advantage but rather the disadvantage of an increasingly drier situation, relative to the height attained. There is no significant shortening or widening of the internodes as a plant climbs or any evidence of leaf or root dimorphism. The normal complement of leaves observed at the apex of the stem in the terrestrial state is retained in the hemiepiphytic state, in plants of the same species. Possibly significant is the fact that the longest internodes in the genus are found in some of these occasional hemiepiphytes. However, no difference in the internode lengths of the appressed and epigaeous portions has been observed. There are otherwise no notable differences in that the vegetative or floral structures of species that are reported as strictly terrestrial and those reported as strictly or occasionally hemiepiphytic.

Stems of taxa with a terrestrial habit can be erect, decumbent, or both (in some species), usually with some portion of the stem subterranean. Of the 42 taxa for which the habit is known, the majority have decumbent stems, with the following 13 having erect stems: *Chlorospatha atropurpurea*, *C. castula*, *C. croatian* subsp. *croatiana*, *C. cutucuensis*, *C. dodsonii*, *C. gentryi*, *C. grayumii*, *C. hammeliana*,

C. ilensis, *C. kolbii*, *C. maculata*, *C. mirabilis*, and *C. morae*. Of these, only the habit of *C. croatianana* subsp. *croatiana*, *C. dodsonii*, and *C. grayumii* is reported as both erect and decumbent. It is interesting to note that taxa with pedate leaf blades are well represented here, eight of the 13 erect-growing species having such blades. Five of these were observed in cultivation (by the authors) for several years and all eventually developed a somewhat decumbent habit while maintaining the more arborescent character of these species. The largest plants in the genus are found in this group, some species attaining heights of 1.5–2 m, with the stems frequently 3–4 cm in diameter and the internodes rarely more than 2 cm long. *Chlorospatha croatianana* subsp. *croatiana* is the giant of the genus, reportedly reaching 2 m in height, although usually less, with the stem portion to 1 m tall. *Chlorospatha dodsonii*, *C. ilensis*, and *C. mirabilis* can be 1.5 m tall. Unfortunately, the habit of collections is too often not recorded. Such is the case with *C. caldasensis*, which is reported as 2 m tall and is probably an erect-growing species. However, the same could not be said for *C. giraldoi*, which can be either terrestrial or hemiepiphytic and was reported as 2 m tall, but has only moderately long petioles and long internodes (2–3.5 cm long), which would accord with a decumbent-growing species in a hemiepiphytic state. The habits of *C. cedralensis* and *C. narinoensis*, both terrestrial species, are not known, but both can be as much as 1.5 m tall. Among the far more numerous decumbent-growing species, only four are known to grow to 1.5 m tall, *C. bogneri*, *C. carchiensis*, *C. litensis*, and *C. sagittata*. Most taxa of *Chlorospatha*, whether the stem is erect or decumbent, are 1 m tall or less, with only 12 species exceeding this height.

In *Chlorospatha*, decumbent stems are epigaeous, occasionally in part rhizomatous, and usually erect for 10–20 cm at the apex. The epigaeous portion has been reported as (10–)25–80 cm long and as much as 1.5 m long in two species, *C. bullata* and *C. sucumbensis*. This portion is not known to retain living leaves and is usually inconspicuous, buried for most of its length beneath the litter on the forest floor. The stems of decumbent-growing species are usually 1–2 cm in diameter, with the internodes usually 1–1.5 cm long, occasionally 4–6(–8) cm long in some species.

Stems of *Chlorospatha* are caulescent, elongated, more or less fleshy and composed mainly of parenchymatous tissue lacking starch (French & Tomlinson, 1981; Madison, 1981). One collection of *C. macphersonii* was reported as having a “somewhat woody stem,” but this would presumably accord with

the typical stem of *Chlorospatha*, as defined here. Stems of erect-growing species become slightly less succulent with age, which would presumably accord with their frequently larger size, as compared to those with a decumbent habit, which remain consistently fleshy regardless of age. The sap of *Chlorospatha* is usually somewhat milky, occasionally transparent or nearly so, and rarely pink. Sap color is known in only 24 taxa. Of these, 18 species have milky sap; four species have transparent sap; and one collection of *C. cogolloi* (Cogollo *et al.* 3160) has pink sap. *Chlorospatha croatianana* var. *enneaphylla* is reported as having either milky or transparent sap, while that of *C. croatianana* subsp. *croatiana* is consistently milky. The sap of *C. oblongifolia* is transparent and becomes gelatinous when the stem is cut.

Internodes are usually short in *Chlorospatha*, approximately 1–2 cm long. Those of the erect-growing species rarely exceed this length and are frequently less than 1 cm long. Although usually 1–2 cm long, longer internodes are found in the decumbent and hemiepiphytic species, frequently more than 2 cm long in strictly decumbent-growing species and occasionally 4.5–8 cm long in those that are occasionally hemiepiphytic, but otherwise decumbent-growing, these having the longest observed in the genus. Internode width is greatest in erect-growing species, usually 3–4 cm in mature specimens but in decumbent and hemiepiphytic species, the diameter of the stem is 2 cm or less in all but 24 species. Of these species, 20 species can have stems 2–3 cm, some of which are the largest in the genus. Only *C. planadensis* consistently has long internodes (3.5–8 cm long). In decumbent and hemiepiphytic species, the diameter of the stem is 2 cm or less in all but 24 species. Of these species, 20 species can have stems 2–3 cm in diameter and only four can have stems 3–3.5 cm in diameter, *C. bayae*, *C. besseae*, *C. boosii* and *C. litensis*, relatively few species compared to the erect-growing species, which frequently have stems 3–4 cm in diameter. In all taxa, internodes are frequently longer in the initial growth made from seeds or bulbils (see discussion below) than in the mature stem. Internodes of juvenile plants of *C. longipoda* can be 4–6 cm long. The possibility of juvenile growth must be considered when delimiting species, the internode length and width being good characters only in adult specimens.

The stem is not stoloniferous and is typically unbranched in *Chlorospatha*, but can be branched through injury. When the apical meristem is severed or severely damaged, a plant can initiate growth from dormant buds or bulbils along the stem, or both. Budding can occur simultaneously at one or several

points along the stem. With the meristem intact, the dormant buds appear as small elevations within a separation of the epidermis and are evident on the stems of all taxa, whether or not they possess bulbils. When bulbils are also present, growth can begin from one or several bulbils as well as from buds. Usually, only one growth near the apex will predominate and growth will cease elsewhere. When bulbils are present, the ultimate dominant growth will be from one of these and not from a bud. These observations were made of 10 species in cultivation: *C. atropurpurea*, *C. boosii*, *C. croatica* subsp. *croatica*, *C. dodsonii*, *C. hannoniae*, *C. ilensis*, *C. kolbii*, *C. longipoda*, *C. plowmanii*, and *C. pubescens*. Bulbils are known to occur in only 13 species: those listed above as well as *C. castula*, *C. portillae*, and *C. sagittata*, species not cultivated by the authors. Madison (1981) included bulbils in his descriptions of *C. atropurpurea* and *C. castula*, but their presence was not noted on the herbarium labels of the collections cited. He cultivated both species at Marie Selby Botanical Garden and probably later observed bulbils in the cultivated specimens. Bulbils were not reported on the label of any herbarium specimen made from a wild collection examined by the authors and only one dried specimen examined possessed bulbils (one), *Luteyn 3155* (DUKE), *C. croatica* subsp. *croatica*. The implication that bulbils usually occur only in cultivation is improbable. An additional explanation for the apparent rarity of observation of bulbils lies in the nature of their attachment, which is tenuous, as in *Xanthosoma* (Madison, 1981), being narrow at the point of attachment, 1–2 mm or less in diameter. The bulbils could be easily lost during the collecting, transporting, drying, and mounting of plants.

Unlike those of *Xanthosoma* (Madison, 1981), the bulbils of *Chlorospatha* are not produced in association with or opposite the axillary bud. The bulbils and dormant buds occur randomly along the stem and are not produced in conjunction with injury but are an integral part of the mature plant. Their tenuous attachment might, to some extent, explain the colonial habit of some species, although bulbils were not observed in all colonial species under cultivation (not in *C. besseae*). Five colonial species in cultivation produced bulbils, *C. boosii*, *C. hannoniae*, *C. longipoda*, *C. plowmanii*, and *C. pubescens*. All had a decumbent habit and developed some growth from bulbils on the erect portion of the stem that was immediately below the soil surface with the bulbils elongating to 2–3 cm in length, in the absence of damage to the meristem and eventually abscising after initiating roots. Other growths occurred from

bulbils that had been dislodged from the parent plant both in cultivation and in the wild, and this appears to be the primary mechanism for growth from bulbils in the erect-growing species that were cultivated but does not explain why these species are not colonial in wild population. It is possible that a colonial habit occurs in these species but has not been reported and could not be determined with certainty in cultivation. In *C. ilensis* and *C. kolbii*, the bulbils below the soil surface exhibited considerable elongation, to as much as 10 cm in the first species and 5 cm in the latter species, without producing leaves or roots. However, when plants were disturbed and the elongated bulbils dislodged, the bulbils would occasionally then develop roots and leaves. This would seem to indicate the possibility of a colonial habit, but in these species, it is also possible that bulbils simply provide a means of survival if the main body of the plant dies. It is noteworthy that when a plant dies and the stem collapses, the bulbils remain viable and attached to the dead epidermis, suggesting that they are perhaps of epidermal origin, as in *Xanthosoma* (Madison, 1981).

Bulbils occur in taxa that are erect-growing (*Chlorospatha atropurpurea*, *C. castula*, *C. croatica* subsp. *croatica*, *C. dodsonii*, *C. ilensis*, *C. kolbii*) or decumbent-growing and colonial or not (*C. boosii*, *C. hannoniae*, *C. longipoda*, *C. plowmanii*, *C. portillae*, *C. pubescens*, *C. sagittata*). *Chlorospatha dodsonii* and *C. longipoda* are the only occasionally hemiepiphytic species that are known to possess bulbils. Bulbils occur only in the basal one third of the stem of *C. dodsonii* and *C. ilensis*, but along the entire length in all other taxa. Another cultivated, mature collection of *C. dodsonii* possessed no bulbils. Bulbils are either exclusively or usually solitary in all taxa discussed here except *C. boosii*, which consistently has bulbils of nearly equal size, in rosette clusters of (one)two to six. In the other taxa, there are occasionally much smaller, collateral bulbils associated with the dominant bulbil, usually only one or two, and these remain small.

The shape of bulbils (on the exposed portion of the stem) can be cylindrical and elongated (*Chlorospatha croatica* subsp. *croatica*, *C. dodsonii*), subglobose (*C. boosii*, *C. plowmanii*, *C. pubescens*, *C. sagittata*), conical (*C. atropurpurea*) or ovoid (*C. hannoniae*, *C. ilensis*, *C. kolbii*, *C. longipoda*, *C. portillae*). When mature, the bulbils can be more or less pointed at the apex or rounded and briefly attenuated, with short internodes approximately 0.5–1.5 mm long. Bulbils are green when emerging, with the outer portions comprised of triangular, scalelike leaves that become sparsely fibrous at the nodes when mature, with the

fibers pale to medium brown, thus resembling miniature stems, which in turn have dormant buds on their surfaces. The largest bulbils were observed in *C. atropurpurea* and *C. croatica* subsp. *croatica*, which were as much as 2 cm long and 1.5 cm diameter in the first species and 2.2 cm long and 1.2 cm diameter in the latter. Bulbils are usually 5–10 mm long and 3–10 mm diameter in the other species.

Most *Chlorospatha* have more or less green, featureless internodes that are glabrous, lack scales, and are not costate, wrinkled, speckled, lineate, or striate. One collection of *C. croatica* subsp. *croatica* (Croat 83606) reportedly had the epidermis peeling and curling back on internodes at the base of the stem, and those of *C. engleri* and *C. sagittata* were reported as occasionally having closely spaced longitudinal grooves near the nodes. It is possible that these and other features exist in collections of additional taxa and have not been reported. However, the fresh coloration, texture, and degree of glossiness provide useful characters, having proven to be consistent within an acceptable range of variation in both wild and cultivated collections. The surface texture and color of living internodes are known for 42 taxa, 32 of which have matte to more or less glossy, green internodes. In 23 of these, the internodes are consistently entirely green, regardless of age, and can be from pale to dark green, yellow-green, olive-green, brownish green, or grayish green, depending on the species. Four of the 32 species, *C. besseae*, *C. bogneri*, *C. longipoda*, and *C. planadensis*, have internodes that are green and occasionally or usually purplish or purple-tinged. Two species, *C. atropurpurea* and *C. queremalensis*, have green internodes that become brown with age, and *C. bayae* has green internodes that become gray with age. Two species, *C. boosii* and *C. hannoniae*, have green internodes that become pale, greenish tan, and weakly scurfy with age, mainly at and around the nodes. *Chlorospatha yaupiensis* is unique in the genus in having red internodes. The nine remaining species have brown internodes and represent eight of the 13 species that are known to be erect-growing: *C. corrugata*, *C. croatica* subsp. *croatica*, *C. cutuensis*, *C. dodsonii*, *C. hammeliana*, *C. ilensis*, *C. maculata*, *C. mirabilis*, and *C. morae*. The habit of *C. corrugata* is not known, but is probably erect, since entirely brown internodes are known to occur only in erect-growing species. The color and texture of the internodes are not known in *C. castula* and *C. gentryi*, both erect-growing species. The only erect-growing species known to have consistently green internodes is *C. kolbii*, and these can occasionally be partially somewhat scurfy and brownish and possibly become

brown with age, as is the case in *C. atropurpurea*. *Chlorospatha queremalensis*, with weakly glossy, green or brown internodes, probably has a decumbent habit, having green internodes 2–4 cm long, which become brown with age. In seven of the erect-growing species, the brown internodes are also reported as somewhat scurfy in texture, meaning that the epidermis is visibly dull and rough, with numerous, minute fissures: *C. croatica* subsp. *croatica*, *C. dodsonii*, *C. hammeliana*, *C. ilensis*, *C. maculata*, *C. mirabilis*, and *C. morae*.

Nodes are always visibly distinct in *Chlorospatha*, but usually otherwise poor in useful features. The internodes between the cataphylls subtending a leaf and the leaf itself are so short that these appear as a single node. A node can be a narrow band ca. 0.5–2 mm wide, which can be slightly raised or not, and slightly minute-fissured, or narrowly, sunken or raised on plants with nodes otherwise in narrow bands. This is possibly explained by the fact that cataphylls are not always produced with foliage leaves in some species, which would presumably result in narrower nodes. The nodes can be green, tan, brown, or brownish in those taxa with green internodes and only brown in those taxa with brown internodes. Younger but mature nodes are green, with the older nodes comparatively more prominently raised, scurfy, and tan to brown or brownish green in three species, *C. boosii*, *C. hannoniae*, and *C. kolbii*.

Roots. According to French (1987), the cortex of the roots of *Chlorospatha* is comprised entirely of thin-walled, unlignified parenchyma cells and lacks resin canals. The roots of *Chlorospatha* are adventitious and can occur at any point along the stem, most frequently immediately above or below the nodes. Roots were frequently seen emerging from within the bases of a petiole sheath in decumbent-growing species.

The number of roots produced is greatest in the portion of the stem in contact with the soil. A substantial subterranean system of mostly fine, fragile, many-branched roots was produced in the species observed in the wild and in cultivation. Branching of the main roots typically does not occur until these make contact with the soil, or in the case of hemiepiphytes, with another substrate, which, in some cases, can be as insubstantial as an accumulation of moss (*Chlorospatha longiloba*). Only moderate lateral branching has been observed on the main roots, with intense ramification proceeding from these branches and all segments accompanied by numerous, fine, short root hairs. Occasionally, the main roots do not branch, but are accompanied by short root hairs. On the erect, exposed portion of the

stem, the unbranched roots are most numerous near the base in both decumbent and erect-growing species, but more numerous in those species with a decumbent habit. The latter also produce more roots than the erect-growing species, on the exposed portion of the stem above the soil surface, these roots being few in the erect-growing species. In erect-growing species, the roots near the base of the exposed stem frequently reach the soil surface and develop normally, with the unbranched, basal portion of the root exposed and becoming brownish with age, whereas the roots higher on the stem reach various lengths, from about 1 cm to occasionally as much as 6 cm, at which point growth ceases. There would appear to be some limiting factor in the length of these exposed roots, none above the basal 6 cm having been observed continuing growth to the soil surface. In cultivation, after growth of exposed roots had ceased, the epidermis of the exposed portion would usually harden somewhat and become brownish. As noted previously, if exposed roots come in contact with a moss-covered tree trunk or suitable substrate, they can develop as they would in the soil.

Little variation in coloration of the fresh, growing roots has been observed, these being almost invariably white to greenish or yellowish cream-colored, occasionally somewhat pinkish.

Cataphylls. The three most taxonomically important character states of cataphylls are whether the cataphylls are deciduous or persistent, if persistent, in what condition they persist, and, in an apparently limited number of species, the consistency with which these are produced in association with foliage leaves. In 63 taxa, these three character states have been determined with some degree of certainty from label notes and observations of living or dried material.

The vegetative cataphylls in *Chlorospatha* are rich in characters, some of which can be difficult or even impossible to determine in dried material because the cataphylls become somewhat fragile on drying, frequently losing the apices during the drying process and having some features obscured. Cataphylls are narrowly triangular to narrowly lanceolate and attached around the circumference of the stem. Typically, fresh cataphylls are thin but firm and occasionally thicker and somewhat fleshy in the larger, erect-growing species. There are no notable differences in the number or features of cataphylls subtending foliage or sympodial leaves. All *Chlorospatha* have marcescent cataphylls that wither more or less intact or partially weakly fibrous on the newest growth and are then either deciduous or to some degree persistent below the apex of the stem.

Cataphylls that are deciduous before withering are not known in *Chlorospatha*. An unusual condition has been reported for *C. bayae*, wherein the cataphylls quickly collapse before drying and are then persistent and more or less fibrous. This possibly occurs in other taxa. Usually two to three cataphylls are produced in association with each foliage and sympodial leaf, occasionally only one and this usually only on juvenile growth. As many as four cataphylls have been observed in *C. croatianae* subsp. *croatiana* and *C. pubescens*. In most taxa, the cataphylls subtending a given leaf exhibit only moderate disparity in length, with the proximal cataphyll being the shortest and all successive cataphylls progressively slightly to moderately longer. In a few species, the disparity in length is more pronounced, as is the case in *C. croatianae* subsp. *croatiana*, in which the proximal cataphyll is only a few centimeters long and the uppermost cataphyll (the third or fourth) is as much as 25 cm long. A similar situation was observed in *C. atropurpurea*, *C. kolbii*, and *C. mirabilis*. Interestingly, all four are erect-growing species. In all *Chlorospatha* with cataphylls subtending foliage and sympodial leaves, the ultimate cataphyll subtending either leaf will be slightly to moderately shorter or longer than the characteristic length of the petiole sheath of the sympodial leaf. The petiole sheath of the foliage leaf is notably shorter than the sheath of the sympodial leaf in most taxa, but the length of the ultimate and longest cataphyll will accord only with the length of the sheath of a sympodial leaf (of similar size) and therefore can be notably longer than the petiole sheath of the foliage leaf. The size of successive leaves and, therefore, the lengths of the petioles and usually the sheathing increase from the time of first flowering until a plant attains its fully mature aspect. This difference can be pronounced in some taxa; therefore, it is best to express the length of the petiole sheath of the sympodial leaf as the ratio of its length to the total length of the petiole, this ratio having proved reliably consistent within an acceptable range in most taxa, regardless of the size of the plant and, therefore, the degree of maturity of the adult petiole. Only the length of the ultimate cataphyll is usually included in descriptions, the lengths of the others having no known significance. The maximum lengths given (in descriptions) do not necessarily correspond to the maximum lengths given for the petiole sheaths because cataphylls are frequently missing or incomplete on herbarium specimens.

Cataphylls are glabrous in all *Chlorospatha* except *C. pubescens*, in which the outer surface of the cataphylls can be either densely crispy-puberulent or

granular-puberulent, in minutely spaced longitudinal rows or densely to sparsely so only along the abaxial rib (or ribs) and major veins, or occasionally not at all (terminology defined below; see Petiole Surfaces). The color and surface texture of cataphylls are rarely reported on herbarium labels and are known in only 23 taxa. In these, cataphylls can be matte or weakly glossy to semiglossy, and in 15 species, usually entirely pale to medium green, rarely dark green (*C. bogneri*, *C. litensis*). Of these 15 species, *C. boosii* can occasionally have cataphylls that are weakly darker green-mottled in narrow transverse bands and those of *C. longipoda* can rarely be similarly purple-mottled. Four species have cataphylls that can be entirely purple or purple-tinged green, *C. atropurpurea*, *C. croatiana* subsp. *croatiana*, *C. ilensis*, and *C. mirabilis*, but which can also be, except in the case of *C. mirabilis*, green with purple mottling in narrow transverse bands. Those of the other three species are consistently green with bands of either darker green mottling (*C. hannoniae*), darker purple mottling (*C. maculata*), or, in the case of *C. kolbii*, either pinkish or green with dark brown, purplish, or black mottling. The cataphylls of *C. sizemoreae* are pink and narrowly transversely purplish lineate, but are green-tinged in the basal one fourth. All taxa with mottled cataphylls also have mottled petioles.

Cataphylls can be 1- or 2-ribbed throughout, 1-ribbed only in the apical one fourth to one half, or not at all ribbed. This character could be determined in only 24 species, and the possibility of error must be considered when only dried material was examined. Ribbing in cataphylls is variable in both shape and number in some species and consistent in others, and therefore would appear to be a weak character on the species level.

The apex of the cataphyll is known in 46 species, although with limited certainty in species known only from dried material, and is consistent on the species level, with a few exceptions that could be attributed to misinterpretation of the dried material. The apex is obtuse with an acumen or apical or subapical apiculum in 31 species, with the acumen or apiculum between 1 mm and 1.5 cm long. There is a tendency toward asymmetry in such cataphylls, with one side usually broader, most prominently so in those species from the eastern slopes of the Andes in Ecuador, in which the widest side is also frequently somewhat auriculate at its apex (*Chlorospatha boosii*, *C. hannoniae*, *C. longipoda*, *C. plowmanii*, *C. pubescens*). A subapical apiculum was observed in *C. litensis*, *C. longipoda*, *C. planadensis*, and *C. pubescens*. In all cases, the apiculum appears to be a continuation of the abaxial rib. In *C. atropurpurea*,

C. croatiana subsp. *croatiana*, *C. kolbii*, and *C. mirabilis*, usually the apex of only the ultimate cataphyll was obtuse with an acumen, the others being more or less acuminate or cuspidate (*C. kolbii*) or even acute at the apex in the case of the short, proximal cataphyll. These four species, as noted above, are among the few that exhibit pronounced disparity in the lengths of the cataphylls subtending individual leaves. The remaining species, which exhibit less disparity, also exhibit little or no disparity in the apical features. Ten species have cataphylls acuminate at the apex: *C. amalfiensis*, *C. betancurii*, *C. engleri*, *C. giraldoi*, *C. huilensis*, *C. jaramilloi*, *C. lehmannii*, *C. macphersonii*, *C. mansellii*, and *C. portillae*. In *C. giraldoi*, the apex can also be cuspidate. Five species can have cataphylls that are cuspidate at the apex: Species 4, *C. grayumii*, *C. pubescens*, *C. ricaurtensis*, and *C. timbiquensis*.

Most *Chlorospatha* produce cataphylls with every foliage and sympodial leaf and all taxa produce cataphylls when initiating growth from bulbils, dormant buds, or seeds. Six species deviate from the norm in one of two ways, either by producing cataphylls inconsistently with foliage leaves or by producing cataphylls only with sympodial growth: *C. besseae*, *C. boosii*, *C. dodsonii*, *C. engleri*, *C. hannoniae*, and *C. mansellii*. Of these, only *C. besseae* has persistent cataphylls, these persisting only at the upper nodes and being ultimately deciduous. All six species usually retain remnants of the old leaf bases as a few short fibers or fragments of epidermis, usually only at the upper nodes. Five of the six species mentioned have been observed in cultivation over a period of five to seven years, except *C. engleri*. *Chlorospatha besseae*, *C. dodsonii*, and *C. mansellii* produce cataphylls consistently with sympodial leaves and inconsistently with what are presumably foliage leaves. It is possible that the cataphylls produced with what are apparently foliage leaves are actually associated with sympodial growth in which the inflorescence bud does not develop; however, the lack of cataphylls with some vegetative growth is unusual. During vegetative growth, the new leaves emerge from the apex of the petiole sheath, usually without an attendant cataphyll. In all three species, the sides of the petiole sheath are more or less convolute, easily supporting and protecting the developing foliage leaf in the absence of a cataphyll. When the plant is flowering, the newest leaf is held within a cataphyll and emerges from the base of the previous growth in which the petiole sheath is occupied by the sympodium. These species are sympatric and apparently closely related, having

many characters in common, and *C. mansellii* is possibly a naturally occurring hybrid between the other two species (see *C. mansellii*). This pattern of cataphyll production would be expected to occur in other taxa but is difficult to determine in dried material. *Chlorospatha bogneri*, which appears to be related to these three species, possibly follows the pattern of *C. dodsonii*. No cataphylls were observed on the foliage leaves of the dried material; however, it is possible that these were produced but were either deciduous or lost in the drying process.

Chlorospatha boosii and *C. hannoniae* flower vigorously between May and September, with cataphylls accompanying each sympodial leaf. During the vegetative growth cycle, between October and April, numerous foliage leaves are produced but no cataphylls. In these two species, the arrangement of the cataphylls subtending the sympodial leaf differs from that observed in any other taxon, cataphylls typically being more or less appressed to the developing and mature leaves in *Chlorospatha*. In these two species, the flowering cycle begins with the development of a leaf subtended by one to three cataphylls. The first cataphyll produced may or may not be appressed to the developing leaf, but, as the leaf develops, the cataphylls become loosely arranged, assuming an erect-spreading position in which none is appressed to the leaf. As this growth matures, a sympodium usually develops at the axil of the already mature growth immediately below, rarely at the axil of the growth associated with the cataphylls. A sympodium will develop in association with this first growth of the flowering season only after subsequent growth has begun or has matured.

Most *Chlorospatha* have persistent cataphylls that remain attached to the stem after withering. Of the 63 taxa in which persistence is known, 12 species have deciduous cataphylls: Species 3, *C. bogneri*, *C. boosii*, *C. dodsonii*, *C. engleri*, *C. hannoniae*, *C. maculata*, *C. limonensis*, *C. mansellii*, *C. nambiensis*, *C. sagittata*, and *C. stellasarrae*. All but three of these 12 species retain remnants of old leaf bases as a few short fibers or fragments of epidermis. Species 3, *C. bogneri*, and *C. sagittata* are not known to retain any portion of the cataphylls or leaf bases. Of the 50 remaining taxa, 22 species have cataphylls that persist more or less intact at most nodes: Species 1, *C. antioquiensis*, *C. bullata*, *C. congensis*, *C. maculata*, *C. giraldoi*, *C. grayumii*, *C. jaramilloi*, *C. kolbii*, *C. lehmannii*, *C. longiloba*, *C. longipoda*, *C. munchiquensis*, *C. narinoensis*, *C. oblongifolia*, *C. planadensis*, *C. portillae*, *C. pubescens*, *C. ricartensis*, *C. sucumbensis*, *C. timbiquensis*, and *C. tokioensis*. Eight of these species also retain some remnants of the leaf bases: *C. antioquiensis*, *C.*

giraldoi, *C. jaramilloi*, *C. longiloba*, *C. longipoda*, *C. oblongifolia*, *C. ricartensis*, and *C. tokioensis*. The more or less intact remnants of the cataphylls can include some exposed fibers or semi-intact remnants. *Chlorospatha munchiquensis* is distinctive in having prominent remnants of the cataphylls that completely obscure the stem, whereas in *C. sucumbensis*, the remnants are intact but short (2–3 mm long), as if broken or possibly cut by the collector. In *C. oblongifolia*, the intact remnants ultimately become fibrous at the lowermost nodes. Fourteen species have cataphylls that persist more or less intact only at a few upper nodes: *C. amalfiensis*, *C. atropurpurea*, *C. bayae*, *C. besseae*, *C. caliensis*, *C. carchiensis*, *C. cutucuensis*, *C. huilensis*, *C. ilensis*, *C. litensis*, *C. mirabilis*, *C. nicolsonii*, *C. queremalensis*, and *C. sizemoreae*. The nodes below can be devoid of remnants or, in the case of *C. bayae*, *C. ilensis*, *C. litensis*, and *C. queremalensis*, retain fibrous remnants. In *C. bayae*, the fibrous remnants on the lower nodes are prominent, obscuring the stem. *Chlorospatha besseae*, *C. carchiensis*, and *C. nicolsonii* also retain some remnants of old leaf bases at the upper nodes. The cataphylls are retained most of the length in a semi-intact, more or less fibrous condition, with the fibers linear, in eight species: Species 4, *C. callejasii*, *C. cogolloi*, *C. gentryi*, *C. hammeliana*, *C. maculata*, *C. macphersonii*, and *C. morae*. In five taxa, the cataphylls are retained only as more or less numerous long, linear fibers at most nodes: *C. caldasensis*, *C. croatiana* subsp. *croatiana*, *C. croatiana* var. *enneaphylla*, *C. kressii*, and *C. yaupiensis*. In *C. caldasensis* and *C. yaupiensis*, these are rather sparse and in *C. kressii* persist only at the upper nodes. The fibers are prominent and usually cover the stem in both varieties of *C. croatiana*. Only a few short, linear fibers are retained along the lengths of the stems of *C. betancurii* and *C. plowmanii*. In *Chlorospatha*, the fibers retained are always more or less linear and usually pale and straw-colored to occasionally medium brown or reddish brown.

Leaves. The youngest part of the stem bears the leaves in all taxa of *Chlorospatha*. The older part of the stem can be devoid of all remnants of leaves and cataphylls or to some degree covered in the intact, semi-intact, or fibrous remnants of both or either the cataphylls or leaves, along most or all of its length or only at the uppermost nodes below the leaf-bearing portion of the stem. Vernation, as defined by Cullen (1978), is supervolute in *Chlorospatha*. Leaves undergo heteroblastic development, a gradual change in morphology from juvenile to adult forms (Grayum, 1990), which is less pronounced in *Chlorospatha* than in other genera of Araceae. In most *Chlorospatha*, the shape of juvenile blades is usually similar to that of

adult blades, with the change in morphology more pronounced in those taxa with mature blades that are pedatisect, pedatifid, trisect, or trifid. Even in species with limited heteroblastic development, some changes are worth noting, particularly considering the fact that numerous species can flower early in their development, before the sympodial leaf has attained the shape associated with the fully mature plant, a situation that could result in confusion when making determinations. Therefore, the term “mature,” as applied here (in descriptions of taxa), refers only to the ultimate aspect of the leaf of a taxon, to the extent that this is known. The leaf subtending an inflorescence sympodium must be considered “adult” as opposed to “juvenile,” but is not necessarily fully mature in its shape. For example, the fully mature leaves of *C. hastata* and *C. litensis* are conspicuously hastate, with long, well-developed posterior lobes that are more or less acute at the apex, but both species can flower with the subhastate and the posterior lobes short (relative to the length of the anterior lobe) and rounded at the apex. These two species also exhibit another commonly observed aspect of heteroblasty in *Chlorospatha*, wherein the pronounced constriction at the base of the anterior and posterior lobes of fully mature blades is weakly expressed or absent in juvenile and less than fully mature blades. Species with sagittate, subhastate, or hastate blades typically exhibit the conditions described above, with some also having juvenile blades ovate and cordate, subcordate, or cordulate at the base, with the posterior lobes much reduced. The latter condition is commonly observed in species from the eastern slopes of the Andes in Ecuador, but has also been observed in *C. dodsonii*, a species from the western slopes in Ecuador, which has markedly hastate mature blades with posterior lobes almost as long as the anterior lobe.

Heteroblasty is most pronounced in taxa with blades that are pedatifid or trifid. The juvenile blades of *Chlorospatha mirabilis*, a trifid species that occasionally has nearly trisect mature blades, can be entire and ovate to elliptical or hastate to subtrifid, with the lateral lobes reduced in length. The lateral segments of juvenile blades, when present, are moderately to conspicuously shorter than the medial lobe in all trifid and trisect species, with little or no change in the width of the confluent portion between segments. Mature blades of *C. kolbii*, a pedatifid species, have 11 to 14(15) segments, but will flower with blades having (seven to) nine segments, whereas the juvenile blades have five to seven segments that can be weakly broader, relative to their length, than those of adult blades. *Chlorospatha croatianae* subsp.

croatiana, typically a 5-lobed species, is somewhat problematic. Most of its mature characters are highly variable, and it is, in fact, the most variable species of *Chlorospatha*. The blades exhibit considerable variation at every stage of development, some of which may or may not be attributable to heteroblasty. Juvenile blades of *C. croatianae* subsp. *croatiana* are 3- to 5-pedatifid, with the segments usually narrow (3 to 4 times longer than wide) and narrowly confluent with adjacent segments, but the segments can occasionally be broad (about 2 times longer than wide), either broadly or narrowly confluent between segments, and, when 3-lobed, have the outer segments auriculate. Specimens with 5-lobed mature blades frequently have less than fully mature blades that are 3-lobed and auriculate on the same plant, indicating that the auricle is a precursor to the 5-lobed form. However, in other large and presumably mature flowering specimens, all blades are 3-lobed and prominently auriculate, suggesting the possibility that the 3-lobed form is also a mature form. Most 5-lobed blades of this species are more or less auriculate and it is possible that these plants could eventually produce 7-lobed blades, but these have never been observed. The juvenile and less than fully mature leaves of the few pedatisect and trisect species are usually respectively deeply pedatifid or trifid, with smaller and fewer segments than mature blades, which are free to the base or have the confluent portion markedly narrow between segments.

Petiole sheathing is usually proportionally shorter in juvenile leaves than in mature leaves, and the characters of the free portion are not usually as clearly articulated. In species in which the entire length of the free portion of the mature petiole is sharply D-shaped and prominently sulcate with the margins acute, these characters will usually be subdued, lacking, or will occur only in some percentage of the apical portion of the juvenile petiole.

No change in surface texture of petioles or blades has been observed in the development from juvenile to mature form.

In terms of adult blade shape, *Chlorospatha* is exceedingly diverse. Leaves are clustered in the apical portion of the stem, usually erect to erect-spreading, and in only a few species are more than five present at one time. The number of leaves and their habit are consistent characters. Sixty taxa have no more than five erect to erect-spreading leaves at one time, nine of which are known only from herbarium specimens with solitary leaves, a condition that is probably coincidental rather than innate. Eight

species can have as many as six to eight leaves, although they can have fewer, such as *C. bogneri*, *C. dodsonii*, *C. engleri*, *C. gentryi*, *C. litensis*, *C. mansellii*, *C. pubescens*, and *C. stellasarreae*. Three species can have as many as 10 to 14 leaves, *C. boosii*, *C. hannoniae*, and *C. plowmanii*, although they can have fewer. *Chlorospatha boosii*, *C. hannoniae*, *C. plowmanii*, and *C. pubescens*, from the eastern slopes of the Andes in Ecuador, are noteworthy in consistently having leaves that are erect, erect-spreading, spreading, and reflexed-spreading on individual plants. All are small, decumbent-growing species that retain leaves along most or all of the length of the erect portion of the stem, thus giving them a somewhat bushy appearance, unusual in *Chlorospatha*.

All leaves of *Chlorospatha* are either fully expanded foliage leaves or cataphylls. Fully expanded leaves can be either foliage leaves or sympodial leaves.

Petioles. Petioles of *Chlorospatha* are usually erect or erect-spreading from the stem, with the developing blades initially extending in the same plane. *Chlorospatha boosii*, *C. hannoniae*, *C. plowmanii*, and *C. pubescens*, small, decumbent-growing species from the eastern slopes of the Andes in Ecuador, are noteworthy in having the petioles erect, erect-spreading, spreading, and reflexed-spreading on the same plant. Petioles of *Chlorospatha* lack a geniculum and are typically soft or spongy to moderately firm. Only the type of *C. maculata* is reported as having a “brittle” petiole. Petioles are usually long relative to blade length, with a long sheath. Thirty-eight species have petioles 1.4 to 2 times longer than the blades. Five species have petioles 2.5 times longer than the blades: *C. callejasii*, *C. ilensis*, *C. luteynii*, *C. mirabilis*, and *C. planadensis*. *Chlorospatha cedralensis* has petioles 3.1 times longer than the blades, the largest ratio in the genus. *Chlorospatha grayumii* and *C. portillae* are the only species in which the blades can occasionally be slightly longer than the petioles. It is noteworthy that all of the larger, erect-growing species have petioles 2 to 2.5 times longer than the blades. Seventeen species have short petioles, only 1 to 1.3 times longer than the blades. Petioles range in length from 10 cm in *C. stellasarreae* to 125 cm in *C. mirabilis*. Forty-seven taxa have mature petioles between 30 and 79 cm long; 10 species have petioles less than 30 cm long; and 11 species have petioles more than 79 cm long. Five of the last species can have petioles 1 m long or more: *C. cedralensis*, *C. croatian* subsp. *croatiana*, *C. ilensis*, *C. mirabilis*,

and *C. sagittata*. Only *C. stellasarreae* has mature petioles less than 20 cm long.

Free portion and cross-section. The free portion of the petiole, that portion above the apex of the sheath, is 7 mm in diameter or less in all but seven species and is usually less than 5 mm in diameter. In Species 1, *Chlorospatha atropurpurea*, *C. corrugata*, *C. croatian* subsp. *croatiana*, *C. dodsonii*, *C. grayumii*, *C. ilensis*, *C. mirabilis*, and *C. sagittata*, this portion can be as much as 1 cm in diameter, but is frequently less. Many taxa are known only from dried material, and measurements of these were estimated based on the known drying characteristics of similar, living taxa.

The variation of the cross-sectional shape in the free portion of the petiole of mature specimens is taxonomically important. Unfortunately, this diagnostic character is frequently omitted from label notes and nothing is known of this character in 27 species. In 29 taxa, the petiole is entirely terete or subterete, or subterete only toward the apex and otherwise terete. Of these taxa, only *Chlorospatha longipoda* can also have the free portion sharply C-shaped. For definitions of petiole cross-sectional shapes, refer to figure 1 on p. 217 in Croat (1983) with the margins more or less acute. In nine of these taxa, the free portion can also be sulcate either the entire length or only near or toward the apex: Species 1, *C. atropurpurea*, *C. besseae*, *C. bogneri*, *C. engleri*, *C. hastata*, *C. limonensis*, *C. longipoda*, and *C. macphersonii*. The entire free portion can be narrowly to acutely sulcate in Species 1, *C. besseae*, *C. hastata*, *C. limonensis*, and *C. longipoda*. The free portion can also be obscurely sulcate or bluntly V-sulcate in *C. longipoda* in which this character is more variable than in most taxa. In *C. besseae* and *C. bogneri*, the free portion can also be sharply V-sulcate, though only toward the apex in *C. besseae*. Obtuse sulcation occurs at the apex in *C. engleri* and *C. macphersonii*. In three species, *C. croatian* subsp. *croatiana*, *C. dodsonii*, and *C. plowmanii*, the free portion can be obtusely D-shaped or terete, and in *C. dodsonii* and *C. plowmanii*, also obtusely sulcate at the apex.

The free portion is usually or frequently sharply D-shaped in five species, *Chlorospatha grayumii*, *C. litensis*, *C. mansellii*, *C. oblongifolia*, and *C. pubescens*, also sharply U-shaped and thicker than broad in *C. grayumii*. That of *C. oblongifolia* can also be sharply C-shaped, and that of *C. pubescens*, obtusely D-shaped. The free portion of *C. litensis* is also obtusely sulcate at the apex and unusual in having the margins of the free portion acutely raised. In *C. mansellii*, the free portion is broadly obtusely

sulcate. Sulcation observed in one collection of *C. pubescens* (L. P. Hannon *et al.* 97-365) is apparently unique in the genus, being narrowly triangular-sulcate, with flared margins that are concave near the apex of the petiole. Of the remaining six species in which this character is known, the free portion is consistently entirely obtusely D-shaped, usually with the margins becoming more or less acute near the apex in five species (*C. boosii*, *C. hannoniae*, *C. mirabilis*, *C. narinoensis*, and *C. ricaurtensis*) and obtusely D-shaped only in the apical one fourth in *C. sizemoreae*. The free portion in *C. hannoniae* is usually U-shaped, with the margins becoming bluntly acute toward the apex, whereas the margins can be acute or acutely raised in *C. mirabilis*. In *C. boosii* and *C. pubescens*, the free portion is narrowly to acutely sulcate or, in the latter species, occasionally obtusely sulcate its entire length.

An obtuse medial rib has been observed in seven species, *Chlorospatha croatiana* subsp. *croatiana*, *C. grayumii*, *C. ilensis*, *C. kolbii*, *C. litensis*, *C. mirabilis*, and *C. oblongifolia*. *Chlorospatha kolbii* can also have lateral ribs that become acute or alate near the apex and are contiguous with a similarly shaped medial rib on the posterior rib. The occurrence of a medial rib is not associated with any particular cross-sectional shape and is found in species with terete, subterete, and obtusely or sharply D-shaped petioles.

Petiole sheath. The length of the petiole sheath, relative to the total length of the petiole, is taxonomically significant, the variability (or not) of the ratio being consistent within a narrow range at the species level in all taxa, with the greatest range occurring in *Chlorospatha mirabilis* in which the petiole sheath is one third to two thirds as long as the petiole, a range of one third of the total length. In the remaining taxa, the range between minimum and maximum lengths of sheathing is less than one fourth of the total length or not at all variable, except in *C. croatiana* subsp. *croatiana* with a range of one fourth to one half of the total length. It is important to note that this applies only to petiole sheathing of sympodial leaves, the sheaths of foliage leaves frequently being significantly shorter and more variable in relative length in most taxa. Only the ratio pertaining to the sympodial leaf is provided in most descriptions and, when possible, the ratio pertaining to foliage leaves. However, the latter character is frequently difficult to determine when only dried material is available. In 50 taxa, the ratio for sympodial leaves falls somewhere between one third and two thirds of total length, with the ratio consistently one third in 13 species, one third to one half in six species, consistently one half in 17

species, one half to two thirds in 10 taxa and consistently two thirds in four species. In *C. atropurpurea*, the ratio is usually one half to two thirds, but can rarely be three fourths. In nine species, the petiole is sheathed three fourths or more of its length, occasionally almost the entire length in some: *C. bogneri*, *C. cedralensis*, *C. cogolloi*, *C. litensis*, *C. macphersonii*, *C. sagittata*, *C. stellaris*, *C. timbiquensis*. In two species, the petiole is sheathed one fourth to one third of its length, *C. gentryi* and *C. oblongifolia*. The petiole is usually sheathed one fourth of its length or less in four species, with that of *C. plowmanii* usually sheathed one fourth, *C. hammeliana* one sixth to one fourth, *C. pubescens* one tenth to one fourth, and rarely to one third in all three species or to one half in different populations of *C. plowmanii* and *C. pubescens*. The petiole of *C. sizemoreae* is sheathed ca. one tenth on both foliage and sympodial leaves.

The sides of the sheath are presumably convolute in most taxa, this condition having been observed in all living species that have the inflorescence held within the sheath and emerging at or near its apex, as is usually the case in *Chlorospatha* and necessary for the containment of the slender and usually relatively long peduncles associated with these taxa. This character usually cannot be determined in dried material, but can be deduced with reasonable certainty from relevant factors. The sheath margins are smooth in most taxa, but are frequently prominently undulate in *C. dodsonii* and rarely so in *C. ilensis* and *C. litensis*. Sheaths with sides that do not overlap is a condition apparently confined to seven species from the eastern slopes of the Andes in Ecuador, which have comparatively short peduncles and the floral sympodium subtended by a sympodial cataphyll that emerges at or toward the base of the petiole sheath of the subtending foliage leaf (see Cataphylls below): *C. boosii*, *C. engleri*, *C. hannoniae*, *C. longipoda*, *C. plowmanii*, *C. portillae*, and *C. pubescens*. In *C. boosii* and *C. hannoniae*, the sides of the sheath are wide and broadly spreading (to 90° midway), appearing winged (Fig. 22B). In the remaining five species, the sides are erect or erect-spreading, occasionally in-rolled along the margins, and occasionally convolute at the apex. It should be noted that sympodial cataphylls are not confined to species from the eastern slopes of the Andes or those that have the sides of the sheath more or less erect. *Chlorospatha longiloba* and *C. yatacuensis*, from the western slopes, have sympodial cataphylls, but the sides of the petiole sheath are convolute.

The apex of the sheath is decurrent onto the petiole in most taxa, free-ending in 18 species and can be

either decurrent or free-ending in eight species. In most species with free-ending sheaths, the condition occurs only in association with sympodial leaves, with the sheath decurrent on foliage leaves. Sheaths are consistently free-ending on both foliage and sympodial leaves in a few species, e.g., *Chlorospatha bogneri*. An unusual condition was observed in living plants of some species from the eastern slopes of the Andes in Ecuador, which possibly occurs in other taxa but is difficult to determine in dried material. In *C. engleri*, *C. longipoda*, *C. plowmanii*, and *C. pubescens*, one side of the sheath can be conspicuously broader than the opposite side, free-ending at the apex and weakly auriculate, with the opposite side decurrent onto the petiole or narrowly confluent with the more free-ending side, which is also true of the vegetative cataphylls in these species. This is consistently the case in *C. engleri*, frequently the case in *C. longipoda* and *C. pubescens*, and rarely so in *C. plowmanii* in which the apex is usually decurrent on both sides. The eight species in which the apex can be either decurrent or free-ending are *C. bullata*, *C. dodsonii*, *C. engleri*, *C. grayumii*, *C. longipoda*, *C. mirabilis*, *C. plowmanii*, and *C. pubescens*.

Petiole surfaces. Petioles in *Chlorospatha* are usually glabrous and matte to semiglossy. Although there are few reports regarding surface texture, most petioles are matte or weakly glossy, with only six of the 27 taxa in which the character is known having semiglossy petioles: Species 1, *C. croatiana* subsp. *croatiana*, *C. longiloba*, *C. maculata*, *C. munchiquensis*, and *C. portillae*. In *C. croatiana* subsp. *croatiana* and *C. longiloba*, the petioles can also be weakly glossy or matte. Only *C. sizemoreae* is known to have a glossy petiole. In nine species, the entire petiole or only the free portion is minutely many-ribbed: *C. bogneri*, *C. cogolloi*, *C. engleri*, *C. kolbii*, *C. litensis*, *C. morae*, *C. pubescens*, *C. sagittata*, and *C. timbiquensis*. Seven species have petioles that are entirely or partially other than glabrous: *C. bogneri*, *C. castula*, *C. corrugata*, *C. engleri*, *C. gentryi*, *C. pubescens*, and *C. yaupiensis*. These species have petioles that are usually to some degree granulose, granular-puberulent, minutely puberulent, crispy-puberulent or scurfy-pubescent, with the puberulence or pubescence usually occurring in longitudinal rows, frequently in association with minute ribs. When the surface is granulose, it appears to be covered with small, angular grains, much like grains of sand. The granular-puberulent indumentum is comprised of minute, acutely angular scales that are more elongated than the elements of the granulose indumentum. The minutely purberulent indumentum is similar but with the scales more elongated and

hairlike. The following terminology is attributed to Grayum (1986), who describes the scurfy-pubescent indumentum as having “more or less flattened, branched, multicellular hairs.” “Crispy-puberulent” is the same condition more weakly expressed, the hairs being shorter, with fewer or no branches. The various indumentums described do not appear to be distinct conditions but rather the same condition expressed in varying degrees of prominence, with the most prominent expression occurring at or toward the apex of the petiole. Invariably, more than one and occasionally all five forms of indumentum occur on individual petioles and typically extend onto the posterior rib. The petioles of *C. gentryi* and *C. pubescens* can be entirely crispy-puberulent or only so in the free portion, or crispy-puberulent with the free portion entirely scurfy-pubescent or only so toward the apex. Scurfy pubescence is known only in these two species. The petioles of the remaining species mentioned can be entirely granulose and granular-puberulent or crispy-puberulent, or partially so only in the free portion or toward the apex, and occasionally not at all. Granular puberulence is weakest in *C. castula*, occurring only briefly near the apex, with the remaining free portion granulose. Some sparse, random granular puberulence has been observed on petioles of some specimens of *C. longipoda*, but the condition was not consistent within single populations or between different populations.

Coloration. Petioles are usually entirely or partially green, with the 46 taxa in which coloration is known almost evenly divided between those with entirely green petioles (lacking mottling) and those that have some or all collections with the petioles green and either purple-tinged or mottled with purple or darker green in narrow transverse bands, with few exceptions. Mottling in narrow transverse bands consists of minute spots and closely spaced, short lineations, creating a reptilian pattern reminiscent of that found in the petioles of *Dracontium* L. and other genera of Araceae. Interestingly, the indigenous Awá people in northern Ecuador call *Chlorospatha hastata* “papa de la culebra,” “culebra” meaning “snake” in the Spanish language (Fig. 23B). The mottling is prominently reptilian in this species. Mottling is typically progressively darker toward the base of the petiole and muted or lacking toward the apex. Twenty-two species usually have consistently entirely pale to very dark green petioles, with those of *C. litensis* rarely being purplish brown toward the base and those of *C. longipoda* rarely being weakly purple-mottled.

Twelve species have petioles more or less green and consistently darker purple- or green-mottled: Species 1, Species 2, *Chlorospatha castula*, *C. engleri*, *C. hammeliana*, *C. hannoniae*, *C. hastata*, *C. huilensis*, *C. kolbii*, *C. kressii*, *C. sagittata*, and *C. sizemoreae*. The color of mottling is not known in Species 2, *C. huilensis*, or *C. kressii*. The label notes for these species indicate only “darker-mottled,” possibly meaning “darker green-mottled.” Dried material of *C. sucumbensis* has similarly mottled petioles, but nothing is known about the color of the petiole or mottling. Coloration of mottling is variable and unusual in *C. kolbii* and can be brown, purplish, or black, with the mottling more pervasive than in most taxa observed, frequently with the transverse bands barely distinguishable. The five species that can have entirely purple petioles also have the most variable petiole coloration known in the genus: *C. atropurpurea*, *C. croatica* subsp. *croatica*, *C. dodsonii*, *C. ilensis*, and *C. mirabilis*. *Chlorospatha atropurpurea* and *C. croatica* subsp. *croatica* can also have green petioles that are purple-mottled in transverse bands, with the latter species having petioles that can also be entirely green, purple-tinged green, purplish brown, or green with gray mottling. The petioles of *C. ilensis* and *C. dodsonii* can also be entirely green, with the sides of the sheath dark maroon on sympodial leaves of one collection of *C. ilensis*, a condition observed in only one other species, *C. nambiensis*. All species known to have mottled cataphylls also have mottled petioles, but it is not known that all species with mottled petioles also have mottled cataphylls. The petiole in *C. croatica* subsp. *croatica*, *C. dodsonii*, and *C. mirabilis* can also be either entirely purple-tinged green for most of the length or with the apex green. Five species have petioles consistently only purple-tinged green: Species 4, *C. bullata*, *C. chocoensis*, *C. limonensis*, and *C. ricaurtensis*. In *C. limonensis*, the petiole is also dark purple-violet-striate-lineate toward the apex. Unusual coloration has been reported in *C. caldasensis* with brown petioles, one collection of *C. croatica* subsp. *croatica* with gray-mottled petioles, *C. huilensis* with pink-tinged green petioles, *C. munchiquensis* with brownish green petioles, and *C. yaupiensis* with reddish pink petioles. The petioles of *C. mansellii* and *C. mirabilis* can have a glaucous bloom toward the base.

Dried petioles can provide additional useful characters. The petioles of 53 taxa dry dark brown to reddish brown or entirely or partially blackish brown, and matte to weakly glossy in 37, weakly glossy to semiglossy in 11, and matte in five. Of these, the petioles of only two species always dry

semiglossy, *Chlorospatha nicolsonii* and *C. queremalensis*. The petiole of *C. kolbii* can also dry brownish gray, that of *C. atropurpurea* purplish, and that of *C. limonensis* purplish only at the apex. An additional nine species have petioles that usually or occasionally dry green or greenish: *C. boosii*, *C. corrugata*, *C. engleri*, *C. hannoniae*, *C. longipoda*, *C. maculata*, *C. mansellii*, *C. plowmanii*, and *C. pubescens*. This drying color is possibly the result of different drying conditions; however, all but three of these species are representative of a distinct group from the eastern slopes of the Amazon in Ecuador (see Infrageneric Relationships) and the tendency to dry green or greenish brown is maintained in these species, even when different driers have been used. The three species not representative of this group are *C. corrugata*, *C. maculata*, and *C. mansellii*, which only occasionally have petioles that dry greenish brown. An unusual condition observed in only eight species appears to be a good character, with all collections of any given species mentioned exhibiting this character. In Species 1, *C. antioquiensis*, *C. betancurii*, *C. hammeliana*, *C. longiloba*, *C. luteynii*, *C. sizemoreae*, and *C. yatacuensis*, the epidermis of the petiole dries entirely or partially separated more or less intact from the main body, semi-transparent, and semiglossy to glossy. The portion that is not separated, if any, is matte to weakly glossy. The petioles of *C. antioquiensis*, *C. luteynii*, and *C. yatacuensis* dry almost black, whereas those of the other species mentioned dry dark brown or reddish brown.

Blades. The blades of *Chlorospatha* emerge in the same plane as the petiole and, at maturity, can be erect, erect-spreading, spreading, or drooping. Most blades are held horizontally (spreading) or drooping at maturity.

Blade texture. The texture of blades in *Chlorospatha* can be thin, thinly coriaceous, subcoriaceous or coriaceous, with the blades of one species reported as “fleshy,” *C. macphersonii*. These terms apply only to the variation observed within the genus, the blades of *Chlorospatha* being comparatively thin for Araceae. Of the 47 taxa in which this character is known, 38 have blades that are thin, thinly coriaceous, or both, with *C. croatica* subsp. *croatica* and *C. dodsonii* occasionally having subcoriaceous blades. Six species have blades that are usually subcoriaceous: *C. hammeliana*, *C. limonensis*, *C. mirabilis*, *C. munchiquensis*, *C. queremalensis*, and *C. sizemoreae*. The texture of the living blades is not known in *C. congensis*, but the blades dry subcoriaceous and it can be reasonably assumed that the texture of the living blades is either coriaceous or subcoriaceous.

Only two taxa are known to have coriaceous blades, *C. lehmannii* and *C. maculata*, with those of the latter species occasionally being thinly coriaceous, as well as those of *C. mirabilis*, which can be thinly coriaceous but are usually subcoriaceous. Almost all taxa of *Chlorospatha* have blades that dry thin to thinly coriaceous.

Blade surfaces. Laminar tissue is always glabrous on both surfaces in *Chlorospatha*. Engler and Krause (1920) describe the upper surface of the blade of *C. kolbii* as “scabra” and “subholosericea.” The upper surface of *Hort. Bull s.n.* (K), presumably a specimen from the original Wallis collection of this species, was examined and no “hairs” were observed. The upper surface is minutely alveolate in the dried material, which could explain their use of the term “scabra,” meaning “rough to the touch.” In all modern collections of this species, the upper surface is more or less velvety, with subhemispherical elevations seen under low magnification (10×), in both living and dried material. The term “velvety” is somewhat misleading and, as applied in this treatment, refers to a perceived effect rather than to a structural condition implying the presence of “hairs.” Eighteen of the 47 taxa in which surface texture is known have the upper surface velvety or matte-subvelvety. The upper surface is matte in 10 species, semiglossy in six species, glossy or occasionally semiglossy in six species, and weakly glossy in six species. The character is consistent in most taxa, with slight variation exhibited in some, such as in those species with matte blades that can occasionally be weakly glossy. Considerable variation has been observed in only a few taxa, the same species that exhibit variation in other characters. In *C. croatianae* subsp. *croatiana*, *C. dodsonii*, and *C. longipoda* (Fig. 32A), the surface can be velvety, subvelvety, matte, weakly glossy, or semiglossy.

In *Chlorospatha*, the upper surface is medium to very dark green, yellow-green or olive-green, with few exceptions. The upper blade surface of *C. caldasensis* is brown, that of *C. atropurpurea* has been occasionally reported as “purplish” medially, and that of *C. sizemoreae* is an unusual grayish green. The dried blades of *C. caliensis* are discoloured and pinkish tan along the major venation on both surfaces, suggesting the possibility of unusual coloration in the living blade. The blades of nine taxa in *Chlorospatha* sect. *Chlorospatha* can be maculate, although this character does not appear to be consistent in those taxa represented by multiple collections: *C. caldasensis*, *C. chocoensis*, *C. cogolloi*, *C. croatianae* subsp. *croatiana*, *C. croatianae* var. *enneaphylla*, *C. kolbii* (Fig. 28A), *C. luteynii*, *C. maculata*, and *C. mirabilis*.

Subepidermal cellular inclusions have been observed in the dried blades of three species. In *C. congensis* and *C. lehmannii*, these are regularly rounded, dark purple-brown speckles that also occur on the lower surface along the veins in the latter species. Cream-colored, linear cellular inclusions were observed only on the lower surface of a developing blade of *C. yaupiensis*. Diffuse, minute green speckles were also observed on the lower surface in *C. congensis*, the nature of which is not known. In *C. cedralensis*, *C. nambiensis*, *C. narinoensis*, and *C. tokioensis*, pale, punctiform, and short, linear raphid cells were observed on the upper surface of dried blades. Diffuse, blotchlike punctuations were observed on the lower surface of the dried blades of the type of *C. grayumii* (30×).

The lower surface of the blades is less frequently reported and thus less well known, but is usually weakly to conspicuously paler than the upper surface and matte to semiglossy, a glossy lower surface having been reported in only four species: Species 3, *Chlorospatha ilensis*, *C. portillae*, and *C. sizemoreae*. Several interesting diagnostic characters have been observed on the lower surface. The lower surface in *C. atropurpurea*, *C. bullata*, *C. castula*, *C. chocoensis*, *C. cogolloi*, *C. hastata* (Fig. 23B), and *C. mirabilis*, is purple, purplish, purple-mottled, or narrowly to broadly marginally discolored (purple) along the midrib and major veins, depending on the species. Of these, only *C. bullata* can also have the surface entirely green. No species from the eastern slopes of the Andes is known to have the lower surface purplish.

In 18 species, the lower surface is consistently conspicuously reticulate, with all orders of venation visibly distinct and usually raised or prominulous in both living and dried material: *Chlorospatha besseae*, *C. bogneri*, *C. boosii*, *C. bullata* (Fig. 8C), *C. corrugata*, *C. dodsonii*, *C. engleri* (Fig. 19D), *C. hannoniae*, *C. limonensis*, *C. longipoda*, *C. macphersonii*, *C. mansellii*, *C. morae*, *C. plowmanii*, *C. pubescens*, *C. sucumbensis*, *C. timbiquensis*, and *C. yaupiensis*. This character is represented in species from both slopes of the Andes in Colombia and Ecuador. Nine of these species exhibit another interesting character, wherein the laminar surface is narrowly colliculate along all veins: *C. besseae*, *C. boosii*, *C. engleri*, *C. hannoniae*, *C. limonensis*, *C. longipoda*, *C. mansellii*, *C. plowmanii*, and *C. pubescens*. In *C. sucumbensis*, the lower surface is also reticulate, but the colliculate border occurs only partially along the tertiary veins and not at all along the reticulate veins. “Colliculate” refers to the densely arranged, minute, rounded elevations comprising this border. In these species, the lower

surface is frequently reported as “matte” when, in fact, usually only the colliculate border is matte and the central portion within the border is usually semiglossy. This is most obvious in the dried material. This character is predominant in the species from the eastern slopes of the Andes in Ecuador, with nine of the 12 species from that region exhibiting this character. In *C. sizemoreae*, the condition is uniquely expressed in that the lower surface of the blade is not reticulate. The tertiary and reticulate veins are neither raised nor prominent but merely visible and bordered by the colliculate blade surface.

The upper surface of the blade is more or less broadly quilted in most *Chlorospatha*, with the midrib, primary lateral veins, and innermost collective vein moderately to deeply sunken, occasionally with the interprimary and some secondary veins less prominently sunken, and the intervening leaf tissue broadly raised. The interprimary and some secondary veins are also moderately sunken on the blades of *C. dodsonii*, creating a wrinkled-quilted effect (Fig. 18B). In some or all collections of eight species, the blade surface is more or less flat and not broadly quilted: Species 2, Species 3, *C. bayae* (Fig. 7A), *C. croatianae* subsp. *croatiana*, *C. hammeliana*, *C. limonensis*, *C. maculata* (Fig. 34B), and *C. mirabilis*. In these, the midrib, primary lateral veins, and innermost collective vein are narrowly or obscurely sunken, etched-sunken or etched, with the intervening blade surface more or less flat. However, the surface can be quilted in some collections of *C. croatianae* subsp. *croatiana*, *C. hammeliana*, and *C. mirabilis*. *Chlorospatha pubescens* typically has broadly quilted blades, but one collection from the northern limit of its range has flat blades. Blades that are quilted or not, as described above, are considered “smooth.” Ten species have other than smooth blades, seven of which have bullate or sub-bullate blades: *C. bullata*, *C. congensis*, *C. engleri* (Fig. 19B), *C. hannoniae*, *C. macphersonii*, *C. morae*, and *C. munchiquensis*, and possibly also *C. huilensis*, which is reported as having all orders of venation “markedly impressed” on the upper surface in some collections. The living blade of *C. congensis* is not known, but the surface of the dried blade is minutely bullate. The blades are rugose in one species, *C. bogneri*, and corrugate in two species, *C. corrugata* (Fig. 15A) and *C. litensis*, consistently so only in *C. corrugata*.

Blade shape. Blade shape is highly diverse in *Chlorospatha* and can be entire, simple and ovate, oblong, cordate, sagittate, subsagittate, hastate, subhastate, trifid, or pedatifid, or compound and trifid or pedatisect. Blades are not known to be pinnately lobed or pinnately compound in *Chlor-*

ospatha. In some cases, blade shape relates to sectional differences, with *Chlorospatha* sect. *Chlorospatha* including all but one of the taxa with blades that are trifid, trisect, pedatifid, or pedatisect. *Chlorospatha* sect. *Orientales* and *Chlorospatha* sect. *Occidentales* include the remaining species, with one species with trifid to trisect blades assigned to the latter section, *C. corrugata*. Most *Chlorospatha* have blades with weakly developed to well-developed posterior lobes, but most are known only from dried material. Therefore, for the sake of consistency, only the shape of dried blades will be considered in these discussions but with the living blade shape provided in taxonomic descriptions, when known. Blade shape appears to be consistent within an acceptable range of variation in most *Chlorospatha*; however, more variation than is typical occurs in three species with posterior lobes, represented by numerous collections from numerous populations in the Amazon drainage, all members of *Chlorospatha* sect. *Occidentales*: *C. longipoda*, *C. plowmanii*, and *C. pubescens*. These and five other species in the section share the same basic stylar morphology and all could probably be easily confused in the juvenile state. The other five species, as well as the remaining species in this section, are known only from one or two collections and it is possible that greater than normal variation in blade shape occurs in these species as well; therefore, it is possible that wide variation in blade shape is normal in most species in section *Orientales* and delimitation of species should be based, for the most part, on floral and other vegetative characters.

Fourteen species with posterior lobes have blades that are more or less narrowly to broadly ovate and cordate, subcordate, cordulate, subsagittate, or occasionally subtruncate at the base. In 16 species with moderately developed to well-developed posterior lobes, the blades are consistently subhastate in seven species, subhastate to hastate in three species, and consistently hastate in six species. The blades are more or less sagittate in 20 species with well-developed posterior lobes, with the shape somewhat variable, as would be expected. These can be narrowly to broadly triangular or have the posterior lobes directed somewhat outward. Three species, *Chlorospatha grayumii* (Fig. 20D), *C. longiloba* (Fig. 31A), and *C. sizemoreae* (Fig. 47A), are unusual in having oblong-elliptic, sagittate blades with the anterior lobes usually conspicuously longer than the posterior lobes. Some collections of *C. longiloba* are subsagittate at the base, with the posterior lobes extremely short (Fig. 29C). The blades of *C. antioquiensis* and *C. bullata* are usually sagittate but can occasionally be ovate-sagittate. Only three

species, *C. oblongifolia* (Fig. 40A), *C. portillae*, and *C. stellarreae* (Fig. 44D), have blades that are entire, lack posterior lobes, and are usually rounded or acute at the base, rarely weakly subcordate or cordulate. The blades of *C. oblongifolia* are usually oblong, but can be ovate-elliptic, as can those of *C. stellarreae*, which are usually merely ovate. Those of *C. portillae* are narrowly ovate.

The apex is usually more or less acuminate in species with undivided blades, and can be briefly, weakly, gradually, abruptly, broadly, or narrowly acuminate, or weakly to prominently long-acuminate. In eight species, the apex can be acute and in eight additional species, apiculate, or also more or less acuminate in all of these. *Chlorospatha atropurpurea* and *C. timbiquensis* exhibit the broadest range of variation, the apex being acute, gradually acuminate, or long-acuminate. The apex is less variable in most species. Numerous species are known only from one or two collections; therefore, the consistency or variability of the character on the species level cannot be determined with certainty.

A useful taxonomic character in species with posterior lobes is the amount of constriction in the area of petiole attachment. Of the 50 species with posterior lobes, there is little or no constriction of the blades in 30 species with weakly to moderately developed posterior lobes, including most species with ovate or sagittate blades as well as numerous species with well-developed posterior lobes. Ten species with well-developed posterior lobes have the blades weakly to moderately constricted, but only on one side in one of these species, *Chlorospatha mansellii*. Blades constricted only on one side were observed in two additional species, *C. carchiensis* and *C. giraldoi*, in which the constriction was moderate or prominent and which occurred only occasionally in the latter species. Moderately to prominently constricted blades are found in *C. grayumii*, *C. hammeliana*, and *C. pubescens*, although the character is not consistent in *C. hammeliana* and *C. pubescens*. The blades of the latter species are usually only moderately constricted, rarely prominently so, and those of *C. hammeliana* can also be weakly or not at all constricted. Six species are quite distinctive, having hastate blades with both the anterior and posterior lobes prominently constricted at their bases or occasionally only moderately so: *C. dodsonii*, *C. hastata* (Fig. 23B), *C. ilensis* (Fig. 26D), *C. litensis*, *C. nambiensis*, and *C. narinoensis*.

Nineteen taxa from Costa Rica, Panama, and western Colombia and Ecuador, but not known from the eastern slopes of the Andes, can have divided and simple (i.e., with the lobes not divided to the base) or

compound leaf blades (i.e., with the segments totally free at the base): *Chlorospatha betancurii*, *C. caldasensis*, *C. callejasii*, *C. cedralensis*, *C. chocoensis*, *C. cogolloi*, *C. corrugata*, *C. croatian* subsp. *croatiana*, *C. croatian* var. *enneaphylla*, *C. gentryi*, *C. hammeliana*, *C. ilensis*, *C. kolbii*, *C. kressii*, *C. luteynii*, *C. maculata*, *C. mirabilis*, *C. morae*, and *C. risaraldensis*. Divided blades occur on all growth in all of these taxa except *C. hammeliana* and *C. ilensis*. Typical blades of *C. hammeliana* are more or less ovate-cordate, but one sterile specimen of what is presumably a collection of this species has a 3-lobed blade. Blades can be hastate or subhastate as well as 3-lobed in *C. ilensis*. Divided blades are usually about as wide as or wider than long and, in most taxa, trifid or pedatifid, deeply lobed, and narrowly to moderately confluent between segments, with the confluent portion usually 0.2–3(–4) cm wide. Nine species have 3-lobed blades, *C. betancurii*, *C. callejasii*, *C. chocoensis*, *C. corrugata*, *C. hammeliana*, *C. ilensis*, *C. maculata*, *C. mirabilis*, and *C. risaraldensis*. Among the pedatifid taxa, *C. caldasensis*, *C. croatian* subsp. *croatiana*, and *C. luteynii* are usually 5-lobed, with *C. croatian* subsp. *croatiana* occasionally having blades that are 3-lobed and prominently auriculate. The blades of *C. croatian* var. *enneaphylla* are 5- to 9-lobed, those of *C. kolbii*, (7- to)9- to 14(15)-lobed, and those of *C. kressii*, 11- to 13(14)-lobed. The blades of only three taxa are consistently compound, but several taxa can consistently or usually have blades that are nearly so and either alate or with the confluent portion less than 4 mm wide or as little as 0.5 mm wide in some species, in dried material: *C. callejasii*, *C. corrugata*, *C. croatian* var. *enneaphylla*, *C. kressii*, *C. maculata*, and *C. risaraldensis*. This portion is usually 5–10 mm wide in *C. mirabilis*, but the blade of one collection is trisect, at least in the dried material. *Chlorospatha corrugata* can also have trisect blades when mature. The blades of *C. cogolloi* are usually trisect, but can be trifid, with the confluent portion usually 1–3 mm wide. The consistently pedatisect species are *C. cedralensis* with five lobes, *C. gentryi* with five to seven lobes, and *C. morae* with five to nine lobes. The degree to which lobes are confluent is consistent within an acceptable range on the species level.

Segments in all taxa with divided blades are usually narrowly to broadly ovate or elliptical, occasionally obovate, but in *Chlorospatha kolbii* and *C. kressii*, these are narrowly oblong-elliptic, lanceolate, or oblanceolate. Segments are also usually more or less acuminate at the apex, occasionally acute, with the medial lobe more or less symmetrical and the lateral lobes weakly to prominently inequilateral, with

the inner sides progressively narrower and the segments progressively shorter toward the outermost lobes in those taxa with more than three lobes. In 3-lobed species, the lateral lobes are usually weakly to moderately shorter than and of approximately the same width as the medial lobe or somewhat narrower. In only a few species are the lateral lobes as long as or slightly longer than the medial lobe, and only in *C. corrugata* and *C. risaraldensis* are they also conspicuously wider than the medial lobe. The comparative lengths and widths of medial and lateral lobes are useful characters in delimiting species. In all taxa with divided blades except *C. chocoensis*, the posterior side of the outermost segment is decurrent onto the posterior rib, at the base. In *C. chocoensis*, this side is decurrent onto the petiole. The nature of attachment on the posterior side of the outermost segments can also be useful and, in some cases, diagnostic. Such is the case in *C. croatian* subsp. *croatiana* and variety *enneaphylla*, with this portion acute toward the base in the latter taxon, but more or less rounded or auriculate in variety *croatiana*. Both can have five lobes, but the nature of attachment of the segments is one of the characters that serves to differentiate the two. These taxa illustrate another useful character, that being the nature of attachment of the lobes at the base, which can be narrow or broad, relative to the width of the lobe. In *C. croatian* var. *enneaphylla*, the attachment is conspicuously narrow, whereas in variety *croatiana*, the attachment is comparatively broad. While lobed leaves in some Araceae, e.g., *Monstera* Adans., are due to necrotic processes in which growth stops and tissue rots away (Madison, 1977), the lobed leaves of *Chlorospatha* result from differential growth of leaf tissue.

Little is known of the blade margins in most taxa, beyond the fact that these are usually smooth, except as regards constrictions in the area of petiole attachment or at the bases of anterior and posterior lobes. Margins are rarely weakly sinuate, this character being obvious but inconsistent in some collections of *Chlorospatha croatian* subsp. *croatiana* and *C. mirabilis*, and so weakly expressed in a few additional taxa as to be insignificant. Several species are known to have blades with more or less undulate margins, these being crispate-undulate in *C. engleri*, *C. gentryi*, and *C. sagittata*, narrowly undulate in *C. kolbii*, *C. kressii*, and *C. plowmanii*, and broadly undulate in *C. longipoda*, *C. plowmanii*, and *C. pubescens*. One collection of the last species has crispate-undulate blades. The presence of undulate margins and the nature of their expression are consistent on the species level. Undulate margins

would be expected to occur in other species, given the thin to thinly coriaceous texture of blades usually observed in *Chlorospatha*.

Posterior lobes. The shape of posterior lobes varies greatly in *Chlorospatha*. In those species with the blades more or less ovate and cordate, sagittate or subsagittate at the base, the lobes are usually broadest at the base and approximately as long as wide, with the apex usually narrowly to broadly rounded or bluntly rounded, e.g., *C. besseae*, *C. limonensis*. The typical blade of *C. hammeliana* is more or less ovate-cordate, with the posterior lobes approximately as long as wide, but the blade shape of this species is one of the most variable in the genus and can also be sagittate or subhastate at the base, with the posterior lobes as much as 2.3 times longer than wide, or sub-3-lobed or 3-lobed. Weakly developed posterior lobes also occur in species with blades that are frequently cordulate at the base, e.g., *C. bogneri*. Species with ovate-cordate and ovate-sagittate blades, and most species with sagittate blades, usually have relatively short posterior lobes, with the anterior lobe about 2 to 3.5 times longer than the posterior lobes, occasionally more than 4 times longer in *C. bogneri*, *C. grayumii*, *C. limonensis*, *C. longiloba*, *C. longipoda*, and *C. macphersonii*. The anterior lobe can be more than 10 times longer than the posterior lobes in *C. longipoda* and as much as 5.4 times longer in *C. longiloba*.

The remaining species with posterior lobes are sagittate, sagittate-subhastate, subhastate, or hastate, with the posterior lobes usually narrowly to broadly triangular or oblong, and acute, bluntly acute, narrowly rounded, or bluntly rounded at the apex, but more or less acuminate at the apex in nine species. The posterior lobes are usually broadest at the base, but can be broadest slightly above the base or midway in some species with the base constricted. The posterior lobes of most species with sagittate or sagittate-subhastate blades are from 1.5 to 2.8 times longer than wide, but those of *Chlorospatha castula* and *C. grayumii* are unusually narrow, usually between 3.1 and 4.3 times longer than wide. Such narrow lobes are usually confined to species with subhastate or hastate blades. The blades of *C. longiloba* can be either sagittate or subsagittate at the base and are unusual in having posterior lobes that can be either short or moderately long, relative to the length of the anterior lobe, with the shorter posterior lobes slightly longer than wide and broadly rounded at the apex, and the longer lobes 2 to 3 times longer than wide and narrowly rounded at the apex.

Species with subhastate to hastate blades usually have narrow posterior lobes, 3 to 4 times longer than

wide, but these can be approximately 5 times longer than wide in *Chlorospatha giraldoi* and *C. narinonensis*. The posterior lobes can be broader in some of these species, less than 3 times longer than wide, notably in species from the eastern slopes of the Andes in Ecuador: *C. plowmanii*, *C. pubescens*, and *C. sucumbensis*. The posterior lobes in these species are also comparatively short for subhastate to hastate species, with the anterior lobe approximately 2 times longer than the posterior lobes, all other such species usually having the anterior lobe only 1.1 to 1.5 times longer than the posterior lobes, or equal in length in some collections of *C. nambiensis*. The posterior lobes of *C. dodsonii* and *C. ilensis* are also broad for hastate species, less than 3 times longer than wide, occasionally as little as 2 times longer than wide. *Chlorospatha planadensis*, a subhastate species, has a broadly triangular blade with conspicuously broad posterior lobes only 1.4 to 1.7 times longer than wide.

The sides of posterior lobes, as defined by the position of the posterior rib, are more or less symmetrical or weakly to moderately unequal in most species of *Chlorospatha*, regardless of blade shape, with the posterior side narrower and the anterior side no more than 2.3 times wider than the posterior side at the midpoint of the lobe, with few exceptions. In 12 species, the sides can be markedly inequilateral, with the outer side between 3 and 6 times wider than the inner side midway, depending on the species: *C. amalfiensis*, *C. besseae*, *C. bogneri*, *C. boosii*, *C. bullata*, *C. hannoniae*, *C. limonensis*, *C. longiloba*, *C. longipoda*, *C. queremalensis*, *C. timbiquensis*, and Species 1, although the ratio can be less. Four species exhibit an unusual condition, wherein the anterior side is narrower than the posterior side, *C. dodsonii*, *C. hammeliana*, *C. ilensis*, and *C. litensis*, although the sides can be more or less symmetrical in some specimens of all four species. Typically, when the posterior lobe is inequilateral, the posterior side is narrower than the anterior side and only on the lateral lobes of divided leaf blades is the posterior side wider than the anterior side. The blades of these four species would, in this sense, appear to be intermediate between taxa with divided blades and those with posterior lobes. The blades of *C. dodsonii* and *C. litensis* are consistently prominently hastate, whereas those of *C. hammeliana* are typically ovate-cordate but can be sagittate, subhastate, sub-3-lobed or 3-lobed. The blades of *C. ilensis* can be subhastate, hastate, or 3-lobed. Interestingly, the morphology of the pistils in both *C. hammeliana* and *C. ilensis* is the same as that otherwise found only in taxa with consistently divided blades, but that of *C. dodsonii* and *C. litensis* is not.

Species with posterior lobes are almost evenly divided between those with the inner side of the lobes decurrent onto the posterior rib at the base and those with that side decurrent onto the petiole. The character is consistent in all but a few species that usually have the inner side decurrent onto the posterior rib, with the rib naked less than 5 mm, but occasionally have the inner side decurrent onto the petiole. Eight species are unusual in having the inner sides of the posterior lobes narrowly confluent at the base, thus obscuring the petiole apex: *Chlorospatha amalfiensis*, *C. antioquiensis*, *C. grayumii*, *C. huilensis*, *C. jaramilloi*, *C. longiloba*, *C. macphersonii*, and Species 4. Although some of these species are known only from single collections, several are represented by multiple collections that would indicate consistency in this character. This condition is frequently difficult to determine in dried material and possibly occurs also in *C. bullata*, *C. giraldoi*, and Species 1, in which the base of the inner side appears to be either decurrent onto the petiole or terminated at the petiole apex.

Sinus shape. Species of *Chlorospatha* with posterior lobes exhibit significant variation in the shape of the sinus of the mature blades, both between and within species; therefore, the character does not appear to be particularly useful on the species level. The shape of the sinus can vary between juvenile blades and mature blades, among different mature blades, and between the living and dried blades of a given species. However, the most common sinus shapes associated with a given species are presented here. The description of the sinus, as presented in this work, is exclusively that of the dried mature blade unless otherwise stated. *Chlorospatha mansellii* has living blades that are subhastate, with the posterior lobes usually overlapping and the sinus rhombic, but which are usually hastate on drying, with the sinus arcuate. In approximately half of all species, the sinus is usually arcuate, narrowly or broadly V-shaped, or V-shaped and narrowly rounded at the apex. *Chlorospatha hammeliana* is a variable species in which the sinus can be narrowly V-shaped, triangular or completely closed, with the posterior lobes overlapping. In *C. pubescens*, the sinus is usually arcuate (for definitions of sinus shapes, see Croat & Bunting, 1979), but can occasionally be oblong. Of the remaining 20 species, the sinus is usually parabolic in seven species, e.g., *C. giraldoi*, lanceolate in five species, e.g., *C. castula*, oblong in four species, e.g., *C. queremalensis*, spathulate in two species, e.g., *C. bayae*, and rhombic in three species, e.g., *C. carchiensis*. The sinus shape can be variable in these species also, as in *C. huilensis*, in which the

sinus is usually parabolic but can be oblong when the sinus is more closed. In all cases, the shape of the sinus can vary according to the degree of maturity of the blades. There is no apparent difference in the shape of the sinus of foliage and sympodial leaves.

Blade size. Blades of *Chlorospatha* are highly diverse in size, but those of most taxa are 20–50 cm long, with most less than 40 cm long. Only six species have blades more than 50 cm long, *C. atropurpurea*, *C. cogolloi*, *C. croatian* subsp. *croatiana*, *C. grayumii*, *C. mirabilis*, and *C. sagittata*, and of these, only *C. grayumii* has blades more than 60 cm long, the longest in the genus. Four species have blades less than 20 cm long, Species 1, *C. bogneri*, *C. stellasarreae*, and *C. timbiquensis*, with *C. stellasarreae* having the smallest in the genus, less than 10 cm long. Most of the largest blades occur in taxa with divided blades; however, the blades of *C. gentryi* and *C. kressii*, pedatisect and pedatifid, respectively, are comparatively small, less than 30 cm long, and approximately as wide as long, as is typical of taxa with divided blades. In some cases, blade size can be a reliable taxonomic character, but the ratio of the length of a blade to its width is more useful and appears to be correlated with the overall shape of the blade. All taxa with divided or hastate blades have blades approximately as wide as long, less than 1.3 times longer than wide, and in some cases, wider than long. More than half of species with subhastate blades would also fall into this category, *C. cutucuensis*, *C. giraldoi*, *C. noramurphyae*, *C. planadensis*, and *C. tokioensis*, although these species can also have blades to as much as 1.5 times longer than wide. *Chlorospatha yaupiensis* is the only species among those with ovate or sagittate blades that has blades approximately as wide as they are long. Twenty-four species have blades approximately 1.5 to 2 times longer than wide, representing all ovate (except *C. yaupiensis*), ovate-cordate (or cordulate), most sagittate, and three subhastate species, these last being *C. atropurpurea*, *C. lehmannii*, and *C. mansellii*. *Chlorospatha atropurpurea* can also have sagittate blades. There is occasional variation of the ratio in these subhastate species, and the blades can be as little as 1.3 times longer than wide or as much as 2.2 times longer than wide. Eight species have blades 2 to 3 times longer than wide, seven with sagittate blades (Species 2, Species 4, *C. caliensis*, *C. carchiensis*, *C. congensis*, *C. engleri*, and *C. huilensis*) and one with subhastate blades, *C. nicolsonii*. The remaining five species are distinctive, all having more or less oblong-elliptic blades. Of these, *C. grayumii*, *C. longiloba*, and *C. sizemoreae* have blades that are sagittate or subsagittate at the base

and between 2.7 and 4.4 times longer than wide. *Chlorospatha oblongifolia* and *C. portillae* have blades that are rounded or acute at the base and 3.5 to 5.6 times longer than wide and (1.3 to) 2.5 to 3.3 times longer than wide, respectively.

Venation of the midribs and major veins. The extent to which the midrib and major veins are sunken (or not) on the upper surface, raised (or not) on the lower surface, and their shape and coloration in both living and dried material are usually consistent within a narrow range in all but a few species, and therefore are taxonomically significant characters. Midribs and major veins on the upper surface of the blades of *Chlorospatha* are usually more or less flat and featureless, with the margins obscure, with three exceptions. The midrib of the living blade is bluntly angular in *C. limonensis* and weakly convex, with the major veins also weakly convex in *C. mansellii*. Only the dried blades of *C. yaupiensis* are known, but the midrib and major veins dry convex toward the base. In those taxa in which the character is known, the midrib is deeply sunken in 23 taxa, moderately sunken in 12 species, and narrowly sunken in five species, with the character consistent in all but a few species. In *C. engleri*, *C. hastata*, *C. litensis*, and *C. longiloba*, the midrib can occasionally be either narrowly or deeply sunken, and in *C. mirabilis*, the midrib can be obtusely or deeply sunken. In *C. croatian* subsp. *croatiana*, the most variable species, the midrib is also variable and can be obtusely, moderately, or deeply sunken. This aspect of the midrib is consistently duplicated in the major veins in all but four species. In Species 1, Species 3, *C. limonensis*, and *C. longiloba*, the midribs are moderately to deeply sunken or narrowly sunken, whereas the major veins are etched, etched-sunken, narrowly sunken, or obtusely sunken and, in all cases, less prominently sunken than the midrib. This condition occurs also in the northernmost population of *C. pubescens*. Only in *C. pubescens* can the midrib and major veins be entirely sparsely crispy-puberulent on the upper surface or only toward the base, these being glabrous in all other *Chlorospatha*. The midrib and major veins on the upper surface are concolorous in most taxa but can consistently or occasionally be weakly to moderately paler in living material of nine species, *C. besseae*, *C. engleri*, *C. hammeliana*, *C. limonensis*, *C. maculata*, *C. mansellii*, *C. mirabilis*, *C. morae*, and *C. ricaurtensis*, and possibly also in *C. bullata* and *C. congensis* in which the midrib and major veins dry weakly to moderately paler than the surface. In *C. sizemoreae*, the midrib is paler than the upper surface and the major veins are moderately darker.

The midrib and major veins on the lower surface exhibit more variation and a number of useful characters that appear to be consistent on the species level, the cross-sectional shape being one of these. This character is not frequently reported on herbarium labels but can usually be ascertained in most cases, with an acceptable degree of certainty, unless the veins dry flattened. No taxon of *Chlorospatha* is known to have the living midrib or major veins flat on the lower surface. In 49 species, the midrib is consistently round-raised on the lower surface, with two exceptions. In *C. mirabilis*, the midrib can also be narrowly angular or acutely raised, and in *C. croatianae* subsp. *croatiana*, the midrib can be acutely raised or convex. “Round-raised” is the most extreme type of raised midrib and appears to be a cylinder attached tangentially to the surface of the leaf (Croat, 1997). The major veins are also round-raised in most species with round-raised midribs but are consistently convex in 15 species with round-raised midribs. In *C. besseae* and *C. bullata*, the major veins are also usually round-raised but can be narrowly raised in the first species and convex in the latter. A few species in this group exhibit interesting variation, with the midrib and major veins round-raised but also obtusely angular in *C. pubescens* and *C. boosii*, the midrib obtusely angular and the major veins acutely angular in the northern population of *C. pubescens*, and the midrib round-raised and the major veins convex and obtusely angular in *C. hannoniae*. The midrib of *C. kolbii* can also occasionally be acutely 1-ribbed medially. Both the midrib and major veins are consistently convex on the lower surface in 12 species, narrowly round-raised in four species, and narrowly raised in two species, with two exceptions. In *C. longipoda*, the midrib and major veins can be narrowly round-raised, round-raised, or convex. In *C. longiloba*, the midrib is usually narrowly round-raised but can occasionally be round-raised, with the major veins either convex or acutely raised.

In most taxa, the midrib and major veins lack ribs and are glabrous or weakly granulose on the lower surface. In nine species, the midrib and major veins are consistently minutely ribbed: *Chlorospatha bogneri*, *C. cogolloi*, *C. engleri*, *C. hastata*, *C. kolbii*, *C. litensis*, *C. morae*, *C. pubescens*, and *C. sagittata*. Eleven species have granulose, granular-puberulent, minutely puberulent, or crispy-puberulent midribs, and major veins: *C. bogneri*, *C. bullata*, *C. castula*, *C. congensis*, *C. corrugata*, *C. engleri*, *C. gentryi*, *C. kressii*, *C. pubescens*, *C. timbiquensis*, and *C. yaupienensis*. Terminology is defined above under section Petiole Surfaces. Interestingly, three of these species

also have minutely ribbed midribs and major veins, *C. bogneri*, *C. engleri*, and *C. pubescens*, with the puberulence occurring along the ribs. In all taxa, if the midrib and major veins are glabrous, ribbed, or puberulent, the given character(s) are usually to some degree duplicated on the posterior rib and petiole and are consistent on the species level.

The color of the midrib and major veins on the lower surface of the blades of living plants is known in 31 taxa and is green in all but five species, *Chlorospatha atropurpurea*, *C. castula*, *C. cogolloi*, *C. hastata*, and *C. mirabilis*, wherein these are more or less purple, as is the lower surface of the blade in most collections. It is likely that all species that have blades that are purplish on the lower surface also have purplish midribs and major veins. Accordingly, it is likely that the midrib and major veins of *C. caldasensis*, which has brown blades, are brown. In 24 of the 26 taxa with green midribs and major veins, these are consistently either concolorous, weakly paler or weakly darker than the lower blade surface, with slight variation in a few species, such as *C. longipoda*, in which these can be either concolorous or weakly darker than the surface. Those of *C. croatianae* subsp. *croatiana* exhibit the most variation, ranging from concolorous to moderately darker than the surface.

The drying color of the midrib and major veins on the lower surface can be a useful character, particularly in cases that deviate from the typical condition observed in 32 species of drying weakly or moderately darker than the surface. The drying color of the midrib and major veins is usually identical and usually varies within a narrow range in a given taxon, with the greatest variation exhibited in *Chlorospatha croatianae* subsp. *croatiana* and *Chlorospatha* var. *enneaphylla*, in which these can dry concolorous, weakly paler or weakly, moderately, or conspicuously darker than the surface. *Chlorospatha lehmannii* is unusual in having the midrib drying concolorous to weakly darker than the surface and the major veins drying moderately to conspicuously darker. The midrib and major veins dry more or less consistently conspicuously darker than the surface, frequently almost black, in 10 species, e.g., *C. luteynii*, purplish in two species, *C. atropurpurea* and *C. hastata*, more or less concolorous to weakly paler or weakly darker than the surface in 21 species, e.g., *C. bogneri*, and usually paler than the surface in five species, *C. bayae*, *C. munchiquensis*, *C. noramurphyae*, *C. sagittata*, and *C. sucumbensis*. The midrib, major veins, and some minor veins also dry more or less wrinkled only in *C. bayae* and *C. congensis*, possibly because the blades in both species dry subcoria-

ceous, unlike those of most taxa, which dry thin to thinly coriaceous.

Primary lateral veins. The primary lateral veins in *Chlorospatha*, previously referred to as “major veins” (see Venation of the Midribs and Major Veins above) and referred to by some authors as “secondary veins” are those that branch pinnately off the midrib and extend uninterrupted and usually unbranched, uniting in a submarginal collective vein. This use of primary lateral veins is consistent with that of Engler and Krause, who referred to these as “nervis primariis lateralibus.”

The primary lateral veins and midrib are typically similar on each surface of the blade, with the primary lateral veins always more or less raised on the lower surface, though frequently somewhat less raised than the midrib. In species with undivided blades, the number of primary lateral veins varies from as few as two to three pairs in *Chlorospatha amalfiensis* and Species 4, to as many as eight to 10 pairs in six species. Thirty-three species have between four and eight pairs of primary lateral veins, and 15 species usually have three to four pairs, including most species from the eastern slopes of the Andes in Ecuador. In taxa with divided blades, the number of pairs of primary lateral veins on the medial and lateral lobes can be the same or different, depending on the taxon, thus rendering the distinction taxonomically significant. The number of pairs are more or less the same on medial and lateral segments in 10 taxa and different in six species. Of the six species with the number of pairs different on the medial and lateral segments: *C. betancurii* has six pairs on the medial and seven to eight pairs on the lateral; *C. caldasensis* has five pairs on the medial and seven to eight pairs on the lateral; *C. callejasii* has five pairs on the medial and nine to 11 pairs on the lateral; *C. corrugata* has four to six pairs on the medial and eight to 10 pairs on the lateral; *C. maculata* has six to eight pairs on the medial and seven to 10 pairs on the lateral; *C. risaraldensis* has six to eight pairs on the medial and eight to 11 pairs on the lateral. *Chlorospatha luteynii* is unusual in occasionally having fewer pairs of primary lateral veins on the lateral lobes than on the medial lobe, the converse being the typical condition. The medial lobe is not entirely known in one species, *C. cedralensis*. *Chlorospatha croatianae* var. *enneaphylla*, *C. kolbii*, and *C. kressii* consistently have two to four pairs on all segments. Most species have four to six pairs on the medial segment, with only *C. mirabilis* having as few as three pairs; *C. croatianae* subsp. *croatiana* and *C. morae* as many as seven pairs; *C. maculata* as many as eight pairs; and *C. cogolloi* as many as 10 pairs, the most known. The number of pairs of primary lateral

veins is consistent within an acceptable range of variation and, therefore, is taxonomically significant.

The primary lateral veins arise from both sides of the midrib of the anterior lobe at between 30° and 65° in most species with undivided blades and on the medial lobes of most species with divided blades. In those species with undivided blades, some of the primary lateral veins can arise at an angle of as little as 15°–25° in 13 species, to as much as 75°–85° in six species, and as much as 90° in three species, these last being *Chlorospatha antioquiensis*, *C. bullata*, and *C. ilensis*. *Chlorospatha munchiquensis* has an asymmetrical anterior lobe and is unusual in having the veins arising at 50°–60° on the broad side and 35°–45° on the narrow side. Among taxa with divided blades, three taxa are unusual in having the veins on both the medial and lateral segments arising only at consistently more acute angles, 15°–30° in *C. croatianae* var. *enneaphylla* and 10°–30° in *C. kolbii* and *C. kressii*. The angle at which the veins arise on the lateral lobes can be the same as, but is usually moderately to markedly greater than, the maximum angle observed on the medial lobe. The lateral veins on the lateral lobes of 3-lobed blades are frequently aggregated toward the base on the posterior side, with some aggregated veins arising at as much as 90° in *C. chocoensis*, 110° in *C. maculata*, and 120° in *C. callejasii*. The angle is usually most acute toward the apex of all lobes or segments, in all taxa, regardless of blade shape. The veins usually ascend in a broad arc and are consistently weakly to moderately arcuate in most taxa, but can be markedly arcuate, straight, or occasionally irregularly ascending in some taxa, meaning that some veins are not evenly curved or straight.

Collective veins. The primary lateral veins ascend toward the margin of the blade and are loop-connected, forming a submarginal collective vein, the innermost of a series of collective veins that run more or less parallel to the margin, with the innermost raised on the lower surface and more or less sunken on the upper surface in a manner similar to but usually less pronounced than that of the primary lateral veins, in both living and dried blades. All but 17 taxa of *Chlorospatha* consistently have only three collective veins. Six species have two to three collective veins. Eleven taxa consistently have three to four collective veins, with three of these taxa, *C. pubescens*, *C. croatianae* subsp. *croatiana*, and variety *enneaphylla*, occasionally having only two. One species, *C. caliensis*, has no less than four collective veins.

The innermost vein is rarely precisely parallel to the margin, but is usually to some degree scalloped,

being indented at the points of union with the primary lateral veins and thus farther from the margin at these points. In 23 species, the collective vein is more or less parallel to the margin or occasionally slightly scalloped, with the indentation slight. Most of the remaining taxa have a weakly to moderately scalloped vein, with the indentation more pronounced. In 10 taxa, the collective vein is markedly scalloped, with the indentation conspicuous, and also markedly remote from the margin, relative to blade size. The collective vein is 3–10 mm from the margin in most taxa of *Chlorospatha*, occasionally 1–2 mm more, with the maximum measurement made from the margin to the union with the primary lateral vein. In those taxa with markedly scalloped collective veins, the maximum measurement can be 18–25 mm in some, to as much as 28 mm in *C. hammeliana*, with the minimum measurement similar to that observed in most taxa but the maximum measurement significantly greater. Several species with markedly scalloped collective veins, *C. kolbii*, *C. kressii*, and *C. limonensis*, have relatively small blades or lobes, and the maximum measurement falls between 8 and 10 mm but is, relative to blade size, markedly remote from the margin. *Chlorospatha gentryi* has a compound blade with relatively small segments and a collective vein that is both markedly scalloped and remote from the margin, as much as 15 mm from the margin. In only five species is the collective vein weakly to moderately scalloped and also markedly remote from the margin, relative to blade size: *C. bogneri*, *C. bullata*, *C. cogolloi*, *C. maculata*, and *C. pubescens*. The outer collective veins are typically aggregated against the margin, with those of *C. bullata* being a noteworthy exception, the vein adjacent to the innermost collective vein also being remote from the margin (on mature blades).

The collective vein typically arises from the base or from one of the lowermost lateral veins of the posterior or lateral lobe, in most taxa, but can arise either from the apex of the posterior rib or one of the lowermost lateral veins on the proximal side of the posterior lobe in six species (i.e., from the lowermost pair of veins on the posterior lobe). In four species, the vein usually arises only from the apex of the posterior rib, *Chlorospatha boosii*, *C. hannoniae*, *C. sizemoreae*, and *C. timbiquensis*. Typically, the collective vein is continuously loop-connected with all preceding lateral veins from its point of origin to the apex of the blade in mature plants. In one collection of *C. bullata* (Croat 50189), the collective vein on one side of the mature blade is continuous from the lowermost basal vein on the outer side (proximal side) of the posterior lobe to the apex of the

anterior lobe and does not intersect the three primary lateral veins on the anterior lobe. Each of the primary lateral veins forms a broad arc that terminates at the midrib apex, a condition occasionally observed in some juvenile blades in other species.

Basal veins. Primary lateral veins arising at the petiolar plexus, the junction of the blade, and apex of the petiole are herein referred to as “basal veins” (see Croat & Bunting, 1979). The first basal vein and occasionally the second usually extend upward into the anterior lobe, with the remaining veins extending into the posterior lobes. The veins extending into the posterior lobes are usually paired, with an equal number on either side of a prominent posterior rib almost as long as the posterior lobe and weakly coalesced into and branch from a posterior rib conspicuously shorter than the lobes. The number of pairs of basal veins ranges from one to nine, with 26 species having three to seven pairs, 13 species having one to three pairs, and only five species having as many as seven to nine pairs, but frequently as few as five or six pairs. Only four species, *Chlorospatha bogneri*, *C. boosii*, *C. hannoniae*, and *C. timbiquensis*, consistently have one to two pairs. Basal veins are lacking in the three species without posterior lobes, *C. oblongifolia*, *C. portillae*, and *C. stellasarreae*.

Posterior ribs. The basal veins are usually to some extent coalesced near their union with the petiole, forming what is herein referred to as the “posterior rib” (see Croat & Bunting, 1979). The first basal vein is usually free to the base at the apex of the petiole and can be briefly fused very near the base with a second basal vein, with the remaining veins loosely coalesced for a short distance into a weak posterior rib or completely coalesced, forming a prominent posterior rib extending from the base almost to the apex of the posterior lobe. Both the number and nature of basal veins and the relative length of the posterior rib are useful taxonomic characters. Species with cordate blades and well-developed posterior lobes can have the posterior rib almost as long as the posterior lobe, e.g., *Chlorospatha besseae*, or conspicuously shorter, e.g., *C. macphersonii*. In *C. hammeliana*, the rib can be much shorter than the posterior lobe, with the basal veins loosely coalesced or almost as long as the posterior lobe, with the basal veins coalesced into a prominent posterior rib. Species with ovate-sagittate blades that are subsagittate or cordulate at the base, such as *C. bogneri* and some collections of *C. longipoda*, typically have relatively short posterior ribs that can be as little as 5 mm long in some

collections and notably shorter than the posterior lobes. The posterior rib is between 6 and 14.5 cm long in 37 species, eight of which can have ribs 14.5–17.5 cm long. In eight additional species, the rib can be as much as 18–24 cm long, with that of *C. sagittata* being as much as 25 cm long and that of *C. ilensis* as much as 28 cm long, the longest known in the genus, although in all cases, the rib can be shorter, depending on the length of the posterior lobe.

An important taxonomic character is the extent to which the posterior rib is naked (or not) along the sinus. Thirty-nine taxa have a naked posterior rib. All taxa with divided blades, except one, have the posterior rib conspicuously naked, to as much as 8 cm on each side in *Chlorospatha croatianae* var. *enneaphylla*. In *C. chocoensis*, the margin of the lateral lobe is decurrent onto the petiole; therefore, the posterior rib is not naked. Most species with well-developed posterior lobes also have the posterior rib naked from a few millimeters to 1.5 cm on each side of the petiolar plexus, or between 2 and 3.5 cm in *C. atropurpurea*, *C. castula*, *C. hastata*, and *C. ilensis*. In *C. hammeliana*, *C. ilensis*, and *C. pubescens*, the posterior rib can be naked or the posterior lobe can occasionally be decurrent onto the petiole, at the base. A number of species with well-developed posterior lobes, the three species with entire blades that are rounded or acute at the base, and most species with ovate-sagittate blades and weakly developed posterior lobes have blades that are decurrent onto the petiole, a total of 22 species. An unusual condition has been observed in eight species in which the laminar tissue is narrowly confluent between the posterior lobes at the base, obscuring the petiole apex: Species 4, *C. amalfiensis*, *C. antioquiensis*, *C. grayumii*, *C. huilensis*, *C. jaramilloi*, *C. longiloba*, and *C. macphersonii*. The condition possibly occurs in three species in which the blades are herein described as decurrent onto the petiole or terminating at the petiole apex, Species 1, *C. bullata*, and *C. giraldoi*, all known only from dried material in which this condition is difficult to determine with certainty.

Lesser order veins. Venation in most *Chlorospatha* is “colocasioid,” with the lesser order venation branching at nearly right angles from the primary lateral veins, then arching strongly toward the margin and usually fusing to form a more or less distinct and usually sinuose interprimary collective vein that unites with the submarginal collective vein (Mayo et al., 1997). However, venation is reticulate in some species. Lesser order veins are herein referred to as “minor veins.” In *Chlorospatha*, the interprimary collective vein is frequently prominently sinuose but can be somewhat straight in some taxa. In a few

species of *Chlorospatha*, there are also intermediate primary lateral veins, herein referred to as “interprimary veins” that arise at the midrib and extend more or less parallel to the primary lateral veins, from the midrib to the submarginal collective vein, without major branching. These are similar to but less prominent than primary lateral veins but are too prominent to be classified as minor veins. There is usually no more than one between each pair of primary lateral veins, but occasionally two may be present. Minor veins arise along the margins of these veins as they do along the margins of primary lateral veins. Some interprimary veins have been observed in 22 species, but occur with some consistency in only eight species, and only in *C. bayae*, *C. corrugata*, *C. morae*, *C. risaraldensis*, and *C. stellasarrae* is their occurrence consistent. Even in these, the veins do not occur between all primary lateral veins.

The most prominent minor veins are the secondary lateral veins that arise from both the midrib and primary lateral veins. These are second order veins based on prominence and thickness (on the lower surface). Secondary veins are structurally indistinct and usually concolorous on the upper surface of the blade and, therefore, characterized only by the extent to which they are sunken or not on that surface. All or some secondary veins are weakly to moderately sunken in valleys in numerous taxa and etched, etched-sunken, or obscure in other taxa. Secondary veins are raised or occasionally in part prominulous on the lower blade surface in all taxa of *Chlorospatha*, usually weakly to moderately so, but prominently so in 11 species, most of which have a reticulate lower blade surface. Secondary veins also dry weakly, moderately, or prominently raised, or in part prominulous on the lower surface in almost all taxa, occasionally in part flattened in some taxa, rarely flat, e.g., in *C. lehmannii*, and usually weakly to moderately darker than the surface, although they can occasionally dry concolorous, weakly paler, or conspicuously darker than the surface in some taxa.

Tertiary veins, third order veins based on prominence and thickness on the lower blade surface, are more or less perpendicular to all of the more prominent veins, including the midrib, and are to some extent visible or otherwise distinct on the lower surface of the blade in most taxa. This character is not frequently reported but can be determined with reasonable certainty in dried material of most taxa. The tertiary veins are raised or prominulous on the lower surface of the blade in 42 taxa, prominently raised in eight species and visibly distinct but entirely flat or in part flat and otherwise prominulous in 20 species. Tertiary

veins are usually obscure on the upper surface, except in those species in which the upper blade surface is bullate, corrugate, rugose, or somewhat wrinkled, in which case they are more or less sunken in valleys. These can occasionally be obtusely sunken, e.g., *Chlorospatha besseae*, or etched or etched-sunken in a few species, e.g., some collections of *C. pubescens*. In no case have these been observed as distinct structures on the upper surface, and, therefore, they are characterized only by the extent to which they are sunken or not on that surface.

Reticulate veins, the smallest veins visible to the naked eye, are more or less perpendicular to all of the more prominent veins, including the midrib, and are to some extent visible or otherwise distinct on the lower surface in approximately half of all taxa. This character is not frequently reported but can be determined with reasonable certainty in most taxa. Reticulate veins dry raised or prominulous on the lower surface of the blade in 25 taxa, visibly distinct in 10 species, and obscure in the remaining species. Reticulate venation is most pronounced in the 18 species in which the lower blade surface is herein described as “reticulate,” meaning that all orders of venation are raised, prominulous, or conspicuously distinct and visible, creating a fine, netlike pattern throughout the lower surface in both living and dried material (Fig. 19D). Reticulate veins are structurally indistinct and usually obscure on the upper surface, except in those species in which the surface is bullate, corrugate, rugose, or somewhat wrinkled, in which case they can be, but are not always entirely, or in part more or less sunken in valleys. The veins can occasionally be obtusely sunken, etched, or etched-sunken in a few species, e.g., *Chlorospatha hannoniae* and *C. pubescens*. Therefore, they are characterized only by the extent to which they are sunken or not on that surface.

In all taxa in which the character is known in both living and dried material, the minor veins are concolorous on the upper surface, with one exception. The secondary veins of *Chlorospatha sizemoreae* are slightly darker than the surface. Another possible exception is *C. bullata* in which all orders of venation dry paler than the upper surface in most collections; however, the living color is not known. All minor veins are usually green on the lower surface in living plants of a given species and can be concolorous, weakly paler, or weakly to moderately darker than the surface, occasionally with the tertiary veins prominently darker. The secondary and some or all of the tertiary and reticulate veins are known to be purple or purplish in *C. atropurpurea*, *C. hastata*,

and *C. mirabilis*, and are probably at least partially so in other species with the lower blade surface purple. Interestingly, in one collection of *C. mirabilis* (Croat 71002), the lower blade surface is entirely dark purple, but the secondary and tertiary veins are green and dry greenish and paler than the surface, which dries purplish. Of the 31 taxa in which the living color of the tertiary veins is known, the veins are darker than the surface in 19 and concolorous in 12. The color of dried tertiary veins is consistently darker than the surface in 34 taxa, either concolorous, concolorous to weakly darker, or concolorous to weakly paler than the surface in 23 taxa, paler than the surface in two species, and weakly darker to weakly paler than the surface in two species. The last two species, *C. bullata* and *C. kolbii*, are unusual in having tertiary veins moderately darker than the surface in living material but concolorous to paler than the surface in dried material. Typically, the color value of the living veins is not so different from that of the dried veins. The reticulate veins of living plants are either darker than the surface or concolorous in about equal numbers of taxa, in the 16 taxa in which the character is known. On drying, the reticulate veins are darker than the surface in 15 taxa, concolorous to weakly darker than the surface in 22 taxa, paler than the surface in three species, concolorous to weakly paler than the surface in one species, and, for the most part, not visible in the remaining species. The extent to which secondary, tertiary, and reticulate veins are sunken (or not) on the upper surface, raised (or not) on the lower surface, and their color in both living and dried blades are more or less consistent in all but a few taxa and, therefore, taxonomically significant characters.

Minor veins on the lower surface are glabrous in most *Chlorospatha*, but are consistently granulose, weakly to conspicuously granular-puberulent, or crispy-puberulent in eight of the 18 species in which the lower blade surface is reticulate, with few exceptions. If all or some of the minor veins are to some degree puberulent, the midrib and major veins of a given species will have a similar indumentum. Species in which some or all of the minor veins are more or less puberulent are: *C. bogneri*, *C. bullata*, *C. corrugata*, *C. engleri*, *C. gentryi*, *C. pubescens*, *C. timbiquensis*, and *C. yaupiensis*, with the character weakest in *C. timbiquensis*. The secondary, tertiary, and reticulate veins are entirely more or less puberulent in six of these species, with the reticulate veins glabrous, but prominent in *C. engleri* and *C. timbiquensis*.

MORPHOLOGY OF REPRODUCTIVE STRUCTURES

INFLORESCENCES

Flowering is morphologically terminal in *Chlorospatha*, although it appears to be axillary, with the stem apex terminating in an inflorescence sympodium or inflorescence bud that does not develop, subtended by a sympodial leaf. New growth is from a bud in the axil of the penultimate leaf below the spathe insertion (in polyphyllous sympodial growth) (Grayum, 1990). Ray (1988) described the inflorescence sympodium consisting of two or more inflorescences as a “gorgonoid monophyllous sympodium,” terminology that appears to accord with the sympodium of *Chlorospatha*. Ray speculated that the inflorescence sympodium was the most advanced state of floral morphology in allowing a plant to mature as many inflorescences with each vegetative article as its resources could support. He further concluded that this pattern possibly allows flowering to become highly seasonal, with a large number of inflorescences being produced with each sympodial leaf during the optimal season for reproduction. According to Ray (1987b: 1368), the (sympodial) “segment consists of an indefinite number of adnate internodes, each newer axis branching from the same side of the lower order axis in a neatly linear arrangement. All of the internodes are greatly reduced. The sympodial leaf subtends the lower end of the segment. The upper end of the segment incorporates the peduncle of the internode terminating the original axis, but also includes an indefinite number of bracteoles in a row, representing multiple axes.” Various terms have been used to describe the modified leaves associated with the inflorescence sympodium and individual inflorescences, resulting in some confusion regarding application of these terms. After discussions with the authors, Michael Grayum suggested a simple, descriptive terminology that eliminates any confusion regarding application of terms and will henceforth be used in this treatment. The “bracteoles” (of Ray) are herein referred to as “inflorescence cataphylls.” In all respects, the modified leaves associated with the sympodium and individual inflorescences are “cataphylls.” In *Chlorospatha*, the leaf subtending a sympodium, the sympodial leaf, is usually a fully expanded foliage leaf, but in some species, the sympodial leaf is a cataphyll, herein referred to as the “sympodial cataphyll.” Inflorescences are always more or less erect in *Chlorospatha*, with each subtended by an inflorescence cataphyll whether the sympodial leaf is a fully expanded foliage leaf or a cataphyll. Sympodial cataphylls and inflorescence cataphylls

are briefly acuminate, cuspidate, or obtuse with an acumen or apiculum at the apex, marcescent, and ultimately deciduous.

In *Chlorospatha*, the floral sympodium arises in association with one of the uppermost leaves, occasionally the uppermost. Flowering associated with the uppermost leaf occurs most frequently in erect-growing species as new vegetative growth is emerging at the base of the petiole sheath of the uppermost leaf. However, flowering can occasionally occur in association with the uppermost leaf in decumbent-growing species as well. In *Chlorospatha*, new vegetative growth typically emerges from the apex of the petiole sheath of the uppermost leaf, and a sympodium is produced in association with one of the leaves immediately below. Only one sympodium is in flower at a given time, but infructescences were frequently observed in association with the leaf or one of the leaves immediately below, occasionally more than one leaf (Figs. 4B, 19D).

In most *Chlorospatha*, the floral sympodium is held within the more or less elongated petiole sheath of a fully expanded sympodial leaf, with individual inflorescences emerging successively at or near the apex of the sheath (Figs. 13D, 26A). In most of these taxa, the length of the petiole sheath of the sympodial leaf will be moderately to conspicuously longer than the petiole sheath of a normal foliage leaf. The sides of the petiole sheath are invariably convolute in these taxa, thereby containing and thus supporting the usually relatively long, slender peduncles and protecting the developing inflorescences. The inflorescence cataphyll subtending each inflorescence is moderately shorter than the peduncle, acutely or obtusely 1- or 2-ribbed abaxially, extremely thin, glabrous, semi-transparent, whitish, or greenish white in color, and rarely observed, usually remaining completely contained within the petiole sheath.

In nine species, the sympodium is subtended by a sympodial cataphyll that emerges at or toward the base of the petiole sheath of the fully expanded foliage leaf subtending the sympodial cataphyll: *Chlorospatha boosii*, *C. engleri*, *C. hannoniae*, *C. longiloba*, *C. longipoda* (Fig. 4B), *C. portillae*, *C. plowmanii* (Fig. 41D), *C. pubescens*, and *C. yatacuensis*. An unusual condition was occasionally observed in *C. boosii* and *C. hannoniae*, wherein the first inflorescence in some sympodia did not appear to emerge from within the sympodial cataphyll. The sympodial cataphyll of a taxon is similar in appearance to a vegetative cataphyll in all respects, being obtusely or acutely 1- or 2-ribbed abaxially, matte to weakly glossy, pale to medium green, thin to thinly coriaceous, and glabrous in all

but one species. In *C. pubescens*, the sympodial cataphyll is frequently sparsely crispy-puberulent along the abaxial rib(s) and longitudinal veins, occasionally not at all, usually in accordance with the indumentum of the vegetative cataphyll of a given collection, although the vegetative cataphyll can be puberulent and the sympodial cataphyll glabrous (on the same plant). Only the sympodial cataphyll of *C. longipoda* is known to be occasionally purple-speckled. Inflorescence cataphylls produced in species with sympodial cataphylls are obtusely or acutely 1- or 2-ribbed throughout or only toward the apex, usually moderately thinner than the sympodial cataphyll, but more substantial than those produced in taxa lacking sympodial cataphylls. Inflorescence cataphylls are glabrous, usually weakly glossy, pale green, and moderately shorter or longer than their respective peduncles, frequently longer in those species with short peduncles (3.5–10 cm long). The number and shape of the abaxial ribs on sympodial and inflorescence cataphylls are not consistent on the species level and therefore not useful characters, which is also true of the vegetative cataphylls in these species. *Chlorospatha plowmanii* and *C. pubescens* usually have both short petiole sheaths and short peduncles; *C. boosii*, *C. hannoniae*, and *C. longipoda* have long petiole sheaths and short peduncles; and most of the remaining species have long petiole sheaths and comparatively long peduncles, *C. engleri*, *C. longiloba*, and *C. yatacuensis*. *Chlorospatha portillae* is unusual in having comparatively short petiole sheaths (to 12 cm long) and long peduncles (to 17.5 cm long). The presence of a sympodial cataphyll does not appear to be correlated with the relative length of the petiole sheath or the orientation of the sides of the sheath, and occurs in vegetatively and floristically diverse species from both slopes of the Andes in Colombia and Ecuador. In *C. boosii* and *C. hannoniae*, the sides of the petiole sheath are wide and broadly spreading (to 90° midway), thus appearing winged (Fig. 22B), and in *C. engleri*, *C. longipoda*, *C. plowmanii*, and *C. pubescens*, the sides of the sheath are more or less erect, occasionally inrolled along the margins and occasionally convolute at the apex. The orientation of the sides is not known in *C. portillae*. The sides of the sheath are convolute in *C. longiloba* and presumably so in *C. yatacuensis* as well, yet the sympodium emerges at or toward the base of the sheath. *Chlorospatha yatacuensis* is included here with reservation, being represented by a single, incomplete herbarium specimen in which the sympodium has been removed from the petiole sheath and is accompanied by a cataphyll that could possibly be a vegetative cataphyll, since there are no

significant differences in the two structures. However, the inflorescences are small relative to plant size, a condition found most frequently in species with sympodial cataphylls. Therefore, this species is included here, with the hope that additional collections will provide pertinent information.

In both forms of sympodial development, the purpose would appear to be provision of support for the typically slender peduncles found in the genus, since the inflorescences of all taxa are held more or less erect. No comparative reproductive advantage is apparent in either form, but it seems likely that some differences in pollination biology or possibly fruit dispersal are involved.

The number of inflorescences per axil does not vary significantly in *Chlorospatha* and would not appear to be a useful character on the species level. Most *Chlorospatha* produce between three and six inflorescences per sympodium, with only two species producing as many as eight inflorescences (*C. croatiana* subsp. *croatiana* and *C. kolbii*), and only *C. portillae*, as many as 10, the maximum number observed in the genus, with the number of inflorescences varying slightly on individual plants and from plant to plant in all taxa. Mature specimens of species herein described as having fewer than three inflorescences in a sympodium probably produce more than one or two. All flower in typical fashion, with inflorescences appearing sequentially at the apex of the petiole sheath, but are known only from dried material with only one to two inflorescences visible or reported on labels. When flowering commences in these taxa, usually only one inflorescence is visible and a collector could mistakenly assume that no more than one inflorescence was present. Due to the nature of flowering in most *Chlorospatha*, the petiole sheath must be dissected in order to determine the full complement of inflorescences in a sympodium. Additionally, when less than sufficient resources are available to a plant or when prevailing climatic or other conditions are less than optimal, some inflorescences may be aborted. No mature specimen of any species observed in the living state (by the authors) produced less than three inflorescences per sympodium. However, most living taxa of *Chlorospatha* observed can flower when quite young and small, with the first flowering usually producing no more than one to two inflorescences. The ability to flower in a less-than-mature state has been observed in 16 species and is probably typical in *Chlorospatha*, but could not be verified in all taxa, many being known only from dried material of presumably mature specimens. In species with sympodial cataphylls, usually more than one and occasionally the entire

complement of inflorescences are visible when flowering commences in habitat. In cultivation, these species tend to grow and flower less vigorously than in the wild, and, consequently, the sympodium can be less obvious.

In species with sympodial cataphylls, inflorescences emerge in quick succession, with each reaching anthesis approximately one to three days after anthesis of the preceding inflorescence. A few relatively large, erect-growing species that lack sympodial cataphylls and flower in the typical manner, e.g., *Chlorospatha atropurpurea*, *C. croatica* subsp. *croatica*, and *C. ilensis*, are unusual and thus noteworthy in producing inflorescences in quick succession, frequently with three to four inflorescences visible at or near the apex of the petiole sheath prior to anthesis of the first inflorescence (Figs. 5B, 16D), at which point only one to several days pass between anthesis of one inflorescence and anthesis of the next. The inflorescences of most *Chlorospatha* that lack sympodial cataphylls emerged in slow progression, with several to many days (approx. five to 10 days) between anthesis of one inflorescence and emergence of the next inflorescence at the apex of the petiole sheath (Fig. 6B). The number of days in this cycle varies in individual plants and from plant to plant in cultivation, apparently in accordance with the health and vigor of the plant and prevailing conditions.

PEDUNCLES

The cross-sectional shape of the peduncle is known in 22 species and is terete, cylindroid (thicker than wide), or both, in most of these taxa and presumably most taxa in which shape is not known. The peduncle can also be obtusely flattened toward the apex, occasionally its entire length, or obtusely D- or U-shaped. An unusual condition was observed in *Chlorospatha kolbii* and *C. mansellii*, wherein the peduncle was broader than thick. In *C. boosii*, the peduncle is obtusely D-shaped in the apical half, with the margins acute toward the apex. The peduncles of *C. mirabilis*, *C. oblongifolia*, and *C. sizemoreae* are obtusely triangular, a condition also observed in the northernmost collection of *C. pubescens*, and in *C. oblongifolia*, also weakly sulcate. The character could not be determined in dried material and is known only from observations of living plants or label notes. With so few taxa represented here, the significance of the character can only be surmised.

Coloration of the peduncle is known in 32 taxa, most of which have peduncles that are pale to medium green, yellow-green, greenish cream, or

cream-colored. Of these, *Chlorospatha atropurpurea* can also have yellow peduncles and *C. pubescens* can also have white peduncles. The peduncles are consistently pale to medium green and entirely or partially weakly to moderately purple-tinged in *C. hannoniae* and *C. limonensis*, occasionally so in *C. longipoda* and *C. pubescens*, and prominently so in *C. portillae* and *C. sagittata*. In *C. bullata*, *C. huilensis*, *C. kolbii*, *C. sizemoreae*, and occasionally *C. ilensis*, the peduncle is green and darker green-mottled in narrow transverse bands, and it is similarly purple-mottled in *C. castula* and *C. hastata*. *Chlorospatha croatica* subsp. *croatica*, the most variable species in the genus, has peduncles that can be entirely purple, green, or yellow-green, or additionally, either darker green- or purple-mottled in transverse bands. In most of the 19 species in which the character is known, the peduncle is matte to weakly glossy, but it is semiglossy in *C. dodsonii* and *C. sizemoreae*, weakly glossy to semiglossy in *C. ilensis*, and glossy in *C. longiloba* and *C. mirabilis*. Peduncles are not ribbed in *Chlorospatha* and are glabrous in all but four species, *C. corrugata*, *C. gentryi*, *C. pubescens*, and *C. yaupiensis*, in which these are usually entirely or in part granular-puberulent, minutely puberulent, or crispy-puberulent (terms defined above under Petiole Surfaces).

In all but nine species of *Chlorospatha*, the peduncle is held within the petiole sheath from its inception through the fruiting cycle and can be slightly shorter or longer than the sheath, with one exception. In *C. hammeliana*, the petiole sheath is 6.5–15.5 cm long, approximately one third of the total length, but the peduncle is 20–40 cm long and only the basal portion is held within the sheath. In all taxa that have most of the peduncle held within the sheath, the lengths of the peduncle and petiole sheath are directly correlated; therefore, the diagnostic character of the ratio of the length of the sheath to total petiole length can also be applied to peduncle length. If the petiole of a sympodial leaf of a given taxon is sheathed one third of its length, the associated peduncles will be approximately one third as long as the petiole. Peduncle length varies slightly within a sympodium but can vary significantly between sympodia on a single plant or different plants of a given taxon, depending upon the maturity of the plant, as can the lengths of the petiole and sheath. Therefore, the ratio of the lengths of the peduncle and petiole is a more useful character, having proven to be consistent within an acceptable range of variation. In the nine species with sympodial cataphylls, the length of the peduncle is not

correlated with the length of the petiole sheath. In this group, species with relatively long sheaths can have long peduncles, e.g., *C. longiloba*, *C. yatacuen-sis*, or short peduncles, e.g., *C. boosii*, *C. hannoniae*, and species with short petiole sheaths can have long peduncles, e.g., *C. portillae*. However, most of the shortest peduncles in the genus occur in these species in which the longest peduncles are no more than 25 cm long (in *C. longiloba*).

The maximum length of the peduncle can be between 20 and 50 cm in 34 taxa and can exceed 50 cm in only eight species, seven of which have peduncles between 50 and 60 cm long, with *Chlorospatha sagittata* having the longest in the genus, 88 cm. Twenty-four species consistently have peduncles less than 20 cm long, 15 of which have peduncles between 12 and 17.5 cm long and nine that have peduncles 10 cm long or less, two of which have peduncles 3–6.5 cm long, *C. plowmanii* and *C. oblongifolia*, the shortest in the genus. The latter species is atypical in being a relatively small plant with a short peduncle that is also broad, 3–4 mm in diameter. Most *Chlorospatha* have peduncles 1–3 mm in diameter. Only 16 species can have peduncles as much as 4 mm in diameter, most of which are large, robust taxa with long peduncles, except *C. oblongifolia*, and, of these, only seven species can have peduncles as much as 5 mm in diameter, *C. besseae*, *C. boosii*, *C. croatian* subsp. *croatiana*, *C. ham-meliana*, *C. mansellii*, *C. planadensis*, and *C. sagittata*. The peduncles of *C. besseae*, *C. boosii*, *C. mansellii*, and *C. sagittata* are more or less cylindroid and only the larger dimension is as much as 5 mm. In all *Chlorospatha*, the peduncle is slightly broadened distally, merging imperceptibly with the spathe tube, and usually narrowest at the base.

SPATHES

The spathe of *Chlorospatha* completely surrounds the spadix prior to anthesis and is invariably narrow, relative to its length, with little or no constriction between the blade and tube. It is more or less narrowly cylindrical, ellipsoid, or ovoid, frequently curved somewhat forward, acute to acuminate at the apex (pre-anthesis) or somewhat cucullate, and thin to thinly coriaceous with the margins slightly thinner and the sides convolute, usually more prominently so on the tube than on the blade. The pre-anthesis spathe is also frequently somewhat deeper (i.e., broadest dorsoventrally) than broad. Although the character is difficult to determine in dried material, the flattened spathe is lanceolate, narrowly ovate, or elliptical in most taxa, narrowly obovate in a few species from the eastern slopes of the Andes in

Ecuador, and weakly to moderately or not at all constricted between the tube and blade. The flattened spathes of *C. atropurpurea*, *C. ilensis*, and possibly others are unusual in having the tube approximately twice as wide as the blade and conspicuously narrower at its union with the blade, which can be weakly constricted at the base or not.

In most taxa, the maximum length of the mature spathe is between 5 and 10 cm, but exceeds 10 cm in 19 species, six of which can have spathes more than 13 cm long: *Chlorospatha bayae*, *C. boosii*, *C. dodsonii*, *C. macphersonii*, *C. mirabilis*, and Species 4. The spathe is no more than 15.5 cm long in five of these species, but can be 20 cm long in *C. dodsonii*, the longest in the genus. However, in all *Chlorospatha*, the length can be less than the maximum stated here. The length can vary significantly between young, developing inflorescences and mature inflorescences; therefore, only the lengths of mature inflorescences have been included in descriptions when possible, maturity occasionally being difficult to determine. In only 12 species is the spathe less than 5 cm long and of these, three species can have spathes less than 4 cm long, *C. engleri*, *C. oblongifolia*, and *C. portillae*, the last two species having mature spathes that can be as little as 3 cm long, the shortest in the genus. The spathe is always longer than the spadix in *Chlorospatha*, usually slightly to moderately so (1–2 cm or less), but prominently so in 11 species with spathes consistently as much as 3–4 cm longer or occasionally 6 cm longer in *C. boosii*.

In almost all taxa, the unopened spathe is 10 to 20 times longer than wide, as much as 25 times longer than wide in a few species, and less than 10 times longer than wide in seven species with relatively short spathes that are approximately 6 to 9 times longer than wide. The ratio is correlated with the typically narrow spathes in *Chlorospatha*, most being between 4 and 9 mm in diameter, with the diameters of the tube and blade more or less equal in all taxa. The spathe can be less than 4 mm in diameter in 11 species with relatively short spathes and more than 1 cm in diameter in nine taxa that represent most of the taxa with the largest spathes in the genus. Of these, *C. atropurpurea*, *C. croatian* subsp. *croatiana*, *C. croatian* var. *enneaphylla*, *C. dodsonii*, and *C. ilensis* can have spathes 1.2–1.5 cm in diameter, the maximum for the genus. Although numerous taxa are known only from dried material, the dimensions of those specimens were determined based on the drying characteristics of similar living spathes.

Of greater significance on the generic level is the ratio of the length and width of the spathe tube, this

being one of the characters that distinguishes *Chlorospatha* from *Xanthosoma* (see Intergeneric Relationships). A precise determination of the apical limit of the spathe tube would be particularly difficult in *Chlorospatha* at or prior to anthesis but can be approximated after staminal anthesis, when the apex is more or less constricted, at which time the tube can be said to terminate at the point of greatest constriction. In *Chlorospatha*, the tube is narrowly ovoid or ellipsoid, decurrent onto the peduncle at the base, and comprises the portion of the spathe that covers the pistillate portion of the spadix and all or most of the sterile staminate portion. The tube is usually 6 to 9 times longer than wide in the genus but can be 10 to 12 times longer than wide in eight species and less than 6 times longer than wide in 18 species, eight of which have tubes less than 4 times longer than wide (3 to 3.7 times longer than wide). Most of the species in which the ratio is small have small inflorescences, with *C. atropurpurea* and *C. ilensis* being exceptions, with ratios 3 times and 4.6 times longer than wide, respectively. Both species have comparatively large inflorescences of large diameter. The tube in *Xanthosoma* is less than 3 times longer than wide, usually 2 times longer than wide or less.

The spathe tube increases somewhat in thickness and persists intact through the fruiting cycle, with the margins convolute on the developing infructescence and more or less separated on the mature infructescence, and the apex directed downward, unless the infructescence is lying on the ground, which is occasionally the case in small, decumbent-growing species from the Amazon Basin. In the 26 taxa in which the infructescence is known, the tube is between 4 and 7.5 cm long in most, between 8 and 10 cm long in six species, and 11–12.5 cm long in *Chlorospatha macphersonii*, the longest in the genus. Three species with the pistillate portion of the spadix comparatively short have presumably mature infructescences less than 4 cm long, *C. corrugata*, *C. cutucuensis*, and *C. longipoda*. The spathe tube is 2 to 2.5 times longer in fruit than at anthesis in 15 species, 1.5 to 1.8 times longer in nine taxa, and less than 1.5 times longer in only two species, *C. corrugata* and *C. cutucuensis*. Infructescences that are less than 1.8 times longer are probably not mature.

The pistillate portion of the spadix in *Chlorospatha* is typically narrow, with few flowers across the axis (as viewed from above; see Spadix, discussion of female portion below) usually between three and five flowers. Consequently, the infructescence is also narrow, between 1 and 1.5 cm in diameter in 14 taxa

and between 5 and 9 mm in diameter in 12 species. The diameter of the tube in fruit is approximately 2–5 mm greater than that of the tube at anthesis, and is approximately 4 to 10 times longer than wide in all but three species: *C. corrugata*, *C. cutucuensis*, and *C. engleri*. The infructescences of *C. corrugata* and *C. engleri* were apparently mature and between 3.4 and 4.5 times longer than wide, whereas that of *C. cutucuensis* was probably immature and 3.1 times longer than wide. Only two species have infructescences more than 10 times longer than wide, *C. munchiquensis* (10.3 times longer than wide) and *C. macphersonii* (11 to 12 times longer than wide).

In most taxa, the spathe tube and blade are of approximately equal length or the blade is slightly longer than the tube, but the tube is longer than the blade in 15 species, usually 5–18 mm longer, but as much as 22 mm longer in *Chlorospatha macphersonii*. In some species, particularly those from the eastern slopes of the Andes in Ecuador, the blade can be conspicuously longer than the tube, usually 5–20 mm longer or occasionally to 3 cm longer, but as much as 6 cm longer in *C. boosii*, 5 cm longer in *C. plowmanii*, 4.5–5 cm longer in *C. dodsonii* and *C. litensis*, and 3.5 cm longer in *C. longipoda* and *C. pubescens*. In those species from the eastern slopes (*C. boosii*, *C. longipoda*, *C. plowmanii*, *C. pubescens*), the marked difference corresponds to a marked difference in the lengths of the pistillate and fertile male portions of the spadix, with the pistillate portion usually being considerably shorter than the fertile male portion, unlike the cited species from the western slopes (*C. dodsonii*, *C. litensis*).

The spathe blade is frequently either entirely obtusely 1-ribbed abaxially or only toward the apex, with the rib frequently acute toward the apex and the margins of the blade more or less in-rolled. The spathe is always glabrous on the inner surface in *Chlorospatha* and usually so on the outer surface, with four exceptions, *C. corrugata*, *C. gentryi*, *C. pubescens*, and *C. yaupiensis*. In *C. gentryi*, the tube is more or less crispy-puberulent on the outer surface, with the indumentum extending narrowly onto the medial portion of the blade. Only the tube is to some degree crispy-puberulent, granular-puberulent, or granulose in the other three species (terminology defined above; see Petiole Surfaces).

The shape of the spathe at anthesis is taxonomically significant but seldom described and, in most respects, difficult to determine in dried material. Certain characters can be determined with some degree of certainty, such as the apex, a reasonably consistent character on the species level, which is acute to weakly, gradually, or abruptly acuminate in

most taxa and cuspidate in 22 species. In *Chlorospatha dodsonii*, the apex can be cuspidate or obtuse with an acumen, and in *C. kolbii*, the apex can be obtuse with an acumen or acute. The blade is also more or less cucullate in 13 taxa, conspicuously so in eight of these: *C. atropurpurea*, *C. boosii*, *C. castula*, *C. croatian* subsp. *croatiana* (Fig. 16C), *C. hammeliana*, *C. hannoniae*, *C. ilensis* (Fig. 26A), and *C. mirabilis*. The spathe of *C. boosii* can exhibit an extreme (in cultivation), wherein the apical half of the blade curves over the spadix (Fig. 9C) and is directed downward, as opposed to more or less outward as it is in other taxa. At other flowerings, the spathe was weakly cucullate in this species. In *Chlorospatha*, the blade is typically more or less erect at anthesis, with the apex oriented in such a way as to shield the open tube from rain, whether cucullate or not. The blade of *C. plowmanii* is usually held in the erect-spreading position at anthesis and does not shield the open tube.

In *Chlorospatha*, the blade is marcescent and typically withers around the fertile male portion of the spadix after staminal dehiscence, then abscises with that portion and, therefore, remains essentially erect, with few exceptions. In *C. corrugata*, *C. limonensis*, and *C. plowmanii*, the blade reflexes after female anthesis, but in *C. plowmanii* (Fig. 41D), the blade quickly withers or is occasionally somewhat caducous and is, in both cases, quickly deciduous, with abscission occurring prior to or coinciding with staminal dehiscence, an apparently unique behavior in the genus. Photographs of *C. corrugata* show the spadix after releasing pollen with the blade persisting in a withered state (Fig. 15B). *Chlorospatha limonensis* is known from a single pickled inflorescence with the blade reflexed but not withered. A fourth species, *C. pubescens*, is inconsistent, with the blade remaining erect after anthesis at most flowerings, or spreading, but not reflexed-spreading, at other flowerings on the same plant. However, it is not quickly deciduous, but persists in the typical manner, abscising with the fertile staminate portion of the spadix.

Most of the information pertaining to spathe shape at anthesis, as described herein, is based on 19 species observed in cultivation (by the authors), over a period of one to seven years, and six additional species known from photographs (*Chlorospatha bogneri*, *C. corrugata*, *C. gentryi*, *C. hammeliana*, *C. huilensis*) or published information (*C. castula*). The 25 species are floristically and vegetatively diverse, representing all known aspects of vegetative and floral morphology in *Chlorospatha* and the full geographical distribution of the genus, but not the

elevational distribution. Presumably most, if not all, pollination strategies are represented in these species. In *C. besseae*, *C. bogneri*, *C. corrugata*, *C. dodsonii*, *C. gentryi*, *C. huilensis*, *C. kolbii*, *C. mansellii*, *C. mirabilis*, *C. oblongifolia*, and *C. sizemoreae*, only the blade opens more or less broadly at anthesis, with the margins directed moderately to prominently outward or forward, depending on the species, and the opening rounded or narrowly to broadly elliptical, accompanied by some expansion of the apical portion, of the tube, thus exposing the fertile staminate portion of the spadix, some or all of the sterile portion, and occasionally as much as one third of the pistillate portion in some species, e.g., *C. besseae* (Fig. 6B). When fully expanded, the spathe is narrowly to broadly more or less funnel-shaped or tubular. In *C. atropurpurea*, *C. croatian* subsp. *croatiana* (Fig. 16C), *C. hastata*, *C. ilensis*, *C. litensis*, and *C. mirabilis*, the entire spathe usually opens between two thirds and three fourths of its length, occasionally nearly to the base, with the margins directed forward or somewhat outward, thus exposing the fertile and sterile male portions of the spadix and part of the pistillate portion, occasionally almost the entire pistillate portion. The shape of the opening is narrowly elliptical, usually with the opening of the tube somewhat narrower than that of the blade. The apex of the tube is not constricted, and only a short portion toward the base remains convolute. The tube is somewhat more expanded at anthesis in all *Chlorospatha*, and in *C. croatian* subsp. *croatiana* and *C. ilensis*, can approach 2 cm in diameter, with the spadix no more than 5–7 mm in diameter, which would suggest the possibility of larger pollinators than were previously considered. When plants are not growing vigorously, the spathe can open only one half of its length, occasionally with the sides of the tube directed inward and the margins touching. In the remaining seven species, the spathe opens narrowly most of its length, occasionally to within 1–2 mm of the base, with the sides directed forward, the margins directed slightly inward, and the opening narrowly elliptical: *C. boosii*, *C. engleri*, *C. hannoniae*, *C. longiloba*, *C. longipoda*, *C. plowmanii* (Fig. 41C), and *C. pubescens*. These are relatively small-growing species with small inflorescences, from the eastern slopes of the Andes in Ecuador, except *C. longiloba*, which is somewhat larger and occurs only on the western slopes.

Spathe color. Coloration of the mature spathe is generally taxonomically significant in *Chlorospatha* and usually varies in value and, in some cases, hue as the spathe develops, reaching ultimate intensity at anthesis. The colors of the spathe tube and blade are

to some degree different in all but 21 taxa, with the blade usually paler than the tube and the transition from one color to the next more or less gradual, never abrupt, though it may initially appear to be so. Although the character is known in fewer than 22 species, the inner and outer surfaces of the tube are usually concolorous or the inner surface is paler, except where otherwise noted, prominently so in a few species. Mature spathe tubes can be consistently or occasionally dark purple or to some degree purple-tinged on the outer surface in 16 species, but are more or less green when developing. The tube can be entirely dark purple outside or only narrowly so at the base, the apex, along the margins, or any combination of these. The color of the blade is not known in all of these species, but in six, the blades are white or cream-colored: *C. amalfiensis*, *C. bayae*, *C. callejasii*, *C. castula*, *C. jaramilloi*, and *C. sagittata*. In *C. longiloba*, *C. longipoda*, *C. plowmanii*, *C. pubescens*, and *C. ricautensis*, both the tube and blade can be purple-tinged, with the blade paler than the tube or not and either entirely purple-tinged or only at the base and along the margins, depending on the species. The spathes of *C. longipoda*, *C. plowmanii*, and *C. pubescens* can also be entirely green, with some collections of *C. longipoda* and *C. plowmanii* exhibiting an unusual condition, wherein the spathe blade is dark purple, with the tube purple-tinged green and paler than the blade. This is consistently the case in *C. hannoniae*, which has a dark maroon blade and maroon-tinged green tube, and *C. portillae* in which the tube and blade are purple-tinged green, but more so prominently on the blade, which is darker than the tube. Although the character is not known in all species with the outer surface of the tube more or less dark purple, the inner surface is also dark purple in *C. bayae*, *C. callejasii*, *C. longiloba*, *C. munchiquensis*, *C. ricautensis*, and *C. sagittata*. The inner surface is usually green in the remaining species, except *C. hannoniae*, in which it is slightly purple-tinged.

In 23 species, both surfaces of the tube are consistently pale to medium green, yellow-green, or greenish cream, and the blade is conspicuously paler and white, greenish white, yellow, cream, yellowish cream, or greenish cream, with four exceptions (see *Chlorospatha gentryi*, *C. atropurpurea*, *C. macphersonii*, and *C. noramurphyae*). The coloration of the tube and blade is more or less the same on the outer surface in 21 species, although the spathe blade is frequently slightly paler than the tube and can occasionally be a different color in one species, *C. antioquiensis*. However, in most of these species, the spathe is entirely pale to dark green, yellow-green,

greenish cream, cream, white, yellow, or yellowish cream on both surfaces, with green being the most common color observed, but the entire spathe is red on the outer surface in *C. noramurphyae*. The inner surface of the tube is occasionally purple or purplish in two of these species, *C. croatianae* subsp. *croatiana* and *C. mirabilis*, and is dark violet three fourths of its length in *C. kressii*.

The biological significance of coloration is not known, but coloration would presumably have some role in pollination, considering the reasonable consistency of the character on the species level. Most inconsistencies can be attributed to the somewhat variable nature of species that are relatively wide-ranging and exhibit variation in numerous characters, within and between populations, such as *Chlorospatha croatianae* subsp. *croatiana* and *C. longipoda*. Similarly, the various surface textures of the inner and outer surfaces of the tube and blade would presumably have a role in pollination, but these are poorly known from living material and in the 20 species in which some or all aspects are known, apparently variable. All surfaces can be matte, weakly glossy to semiglossy, or glossy, with the texture of the tube and blade more or less the same on the outer surface in 12 species and occasionally glossy in only one of these, *C. mirabilis*. The outer surface of the tube is glossier than that of the blade in five species and that of the blade is glossier than the tube in four species. The inner surface of the tube is usually somewhat glossier than the outer surface and frequently semiglossy to glossy, but can be the same as the outer surface. Only that of *C. kolbii* is known to be matte on the inner surface. The inner and outer surfaces of the blade can similarly be the same or have one surface glossier than the other, but unlike those of the tube, there is no apparent tendency for the inner surface of the blade to be glossier than the outer surface and it can, in fact, be matte in 11 species.

SPADIX

Chlorospatha is monoecious, with a more or less cylindrical spadix with naked, unisexual flowers lacking a perigone and arranged in spirals. The spadix can be slightly to conspicuously shorter than the spathe and is, for the most part, contained within it at anthesis, although in some taxa the spadix can curve somewhat forward, e.g., *C. ilensis*, *C. longipoda*. The axis is typically more or less straight, but in some species, the pistillate portion is curved somewhat forward and the staminate portion is erect, e.g., *C. plowmanii*. The spadix in *C. congensis* is apparently unique in curving forward at the base, with the

remainder of the pistillate and staminate portions recurved midway, then back again, thus rendering the apex erect. The apex is consistently either bluntly acute or narrowly rounded in 44 taxa or can be either in five species. The spadix is sessile in most taxa, but is consistently prominently stipitate, with the stipe between (5–)7 and 18 mm long in four species (*C. atropurpurea*, *C. hastata*, *C. kolbii*, *C. kressii*), weakly (1–3 mm) and somewhat inconsistently so in five species, and either moderately stipitate or sessile in *C. croatianae* subsp. *croatiana*. The stipe and axis are green in *C. kolbii* and dark violet in *C. kressii*, with coloration serving as a diagnostic character in these quite similar species. The axis can be white or green in *C. dodsonii* and is dark maroon in *C. sagittata*, which is, interestingly, also the color of the ovaries in this species. An unusual condition was observed in *C. hastata* and *C. luteynii*, both of which are stipitate, wherein the stipe emerges from a sheathlike structure on the spathe, with the sides of the sheath approximately 1 mm wide.

The female flowers are borne on the basal portion of the spadix and the fertile male flowers on the apical portion, with the fertile portions usually separated by a sterile portion that bears distinctive flowers. Occasionally, a few synandrodia are present at the apex of the fertile staminate portion, which are morphologically similar to the synandria, but usually not as deeply lobed, if at all, and lack microsporangia. What appeared to be several free staminodes were observed near the apex in *Chlorospatha atropurpurea*, which had the typical purple coloration of the sterile flowers found in this species and were quite distinct from the cream-colored synandria. The spadix is consistently adnate to the spathe at the base for half or more of the length of the pistillate portion of the spadix in 52 species, in 19 of which it is fused the entire length of that portion and in eight also frequently all or part of the sterile staminate portion. In most of the remaining taxa, the pistillate portion is adnate for one fourth to one third or less of its length but is adnate one fourth to one half of its length in two species. Interestingly, in all prominently stipitate species, the spadix is adnate only along the stipe or occasionally also narrowly (1–2 mm) onto the pistillate portion at the base. The degree to which the spadix is fused to the spathe is taxonomically significant, being consistent in 52 taxa, with the amount of variation less than one fourth of the total length of the pistillate portion in all but six of the remaining species in which the ratio varies by one fourth of the total length. Of these six species, *C. croatianae* subsp. *croatiana*, the most variable species in all respects, is the only one in which the ratio

varies by more than one fourth of the length of the pistillate portion and is either not adnate to the spathe or is adnate for one fifth to three fifths or three fourths of its length. In all taxa, the measured length of the adnate portion can vary significantly between inflorescences on a plant or between plants of a given taxon, according to the maturity of an inflorescence or plant, with the ratio of the adnate portion to the total length of the pistillate portion remaining reasonably consistent and therefore serving as a better character.

The total length of the spadix, though somewhat variable depending on the maturity of plants, is a useful character on the species level when only maximum length of mature specimens is considered. Total length is known in 60 taxa and in 37 of these the maximum length of the spadix is between 5 and 9.5 cm. The spadix can exceed 10 cm in length in 10 species and can be as much as 12 cm long in *Chlorospatha bayae*, *C. macphersonii*, and *C. ricaurtensis*, and as much as 16.5 cm long in *C. dodsonii*, the longest in the genus. In 13 species, the spadix is consistently less than 5 cm long and can be as little as 2.2–2.3 cm long on mature inflorescences of *C. oblongifolia* and *C. portillae*. Regardless of length, the spadix is relatively narrow in all taxa, as would be expected in the typically narrow inflorescences of *Chlorospatha*, and is 4–6 mm in diameter (measured usually midway, but closer to the apex when spadix is clavate) in 40 taxa, 6.5–7 mm in *C. croatianae* subsp. *croatiana* and *C. sagittata*, and as much as 8 mm in *C. dodsonii*, the largest in the genus. In 22 species, the spadix is less than 4 mm in diameter and is only 1.5–2 mm in diameter in *C. stellasarreae*.

The comparative lengths of the three portions of the spadix have greater taxonomic significance than actual lengths in *Chlorospatha*. Admittedly, numerous species are known from only one or two collections; however, in the equally numerous taxa known from multiple collections representing more than one to many populations, this character is consistent on the species level and would appear to represent the typical rather than exceptional condition. The fertile male portion is invariably densely flowered in *Chlorospatha* and shorter than the pistillate portion in 19 species (to 2 cm shorter in *C. macphersonii*), approximately equal in length in 16 taxa, moderately longer (ca. 1 cm longer or less) in 17 species and conspicuously longer in four species in which it can be between 2 cm (*C. hannoniae*, *C. mansellii*) and 3 cm (*C. boosii*, *C. luteynii*) longer. The fertile male portion is more or less cylindrical in 24 taxa, cylindrical to somewhat tapering in four taxa, consistently tapering in 14, ellipsoid in seven species, and clavate in 11 species in which this

portion can also be tapering. Coloration of the fertile male portion is diverse in *Chlorospatha* and known in 48 taxa, with the character more or less consistent in all but a few. The fertile portion is consistently white, creamy white, or cream-colored in 17 taxa, somewhat variably white, cream, or weakly yellowish or greenish in 12 species, bright orange in five species, and reportedly brown in three species, this last color being somewhat questionable. The fertile male portion has been observed as weakly brownish after staminal anthesis; however, it abscises several days after staminal anthesis and the authors have not observed what would be considered a brown fertile portion at anthesis, although the first author reported this portion as "pale yellow-brown" in *C. bayae*. Yellow or creamy yellow fertile portions were reported in six species, or occasionally cream-colored in some of these, with *C. huilensis* having this portion either white or dark yellow. Unusual coloration was reported in some species, with the fertile portion pink in *C. noramuphyae*, green in *C. gentryi*, and dark purple-violet in *C. limonensis*. A dark purple fertile portion is known in only one collection of one other species, *C. croatianae* subsp. *croatiana*, in which this portion can also be white, cream, greenish cream, or yellowish, with this species and *C. antioquiensis* exhibiting the most variation in the genus, with the latter species having the fertile portion red, yellow, or green.

Coloration of the sterile portion is seldom reported and it cannot be assumed that it is usually the same as that of the fertile portion, although this is apparently frequently the case in taxa in which the fertile portion is white or cream-colored. Even in some of these (e.g., *Chlorospatha hannoniae*, *C. plowmanii*, *C. pubescens*), the sterile portion can be either purplish or white to cream-colored, with the fertile portion white or cream-colored. In *C. besseae*, *C. dodsonii*, and *C. mansellii*, the fertile portion is bright orange and the sterile portion a combination of cream and yellow to yellow-orange. More striking differences were observed in other species: the fertile portion more or less cream-colored and the sterile portion dark purple to maroon in *C. atropurpurea*, *C. castula*, and *C. hastata*; the fertile portion somewhat cream-colored and the sterile portion pink or bright orange in *C. longiloba*; and the fertile portion yellowish cream and the sterile portion pink in *C. sagittata*, which is also true of one collection of *C. croatianae* subsp. *croatiana*. The sterile portion is green in *C. mirabilis* and yellow in *C. corrugata*. Although the coloration of the two portions can intensify somewhat as the spadix develops toward anthesis, there is no notable change in that of either

portion at anthesis. The drying color of the sterile portion is usually weakly to conspicuously different from that of the fertile portion and can be darker or paler, depending on the taxon. The colors themselves and their juxtaposition to the different colors of the other portions would presumably have some role in pollination, as would the different surface textures observed, although the latter character is poorly known. The fertile and sterile portions can be matte, weakly glossy, semiglossy, or glossy. In *C. boosii* and *C. hannoniae*, which are similar, sympatric species, the fertile and sterile portions are usually similarly colored, but those of the latter species are glossy and those of the first, matte.

The sterile portion of the spadix and the arrangement of the sterile flowers exhibit considerable diversity in *Chlorospatha*, providing a number of useful and reliable characters on the species level. The characters cited here are reasonably consistent in all taxa, with considerable variation occurring in all characters only in *C. croatianae* subsp. *croatiana*, including the length of the sterile portion, which can be short, long, or absent (3–17 mm long), relative to the length of the other two portions in this species. The length of the sterile portion ranges between zero and 1–2 mm or to as much as 2.7 cm (*C. hastata*) in *Chlorospatha*, exceeding 1.6 cm in only 10 taxa, but is significant only relative to the lengths of the other two portions. In most *Chlorospatha*, the sterile portion is moderately to conspicuously shorter than the pistillate and fertile male portions and can be only one to a few millimeters long in approximately 10 species with either long or short spadices. The sterile portion is only a few millimeters long in *C. dodsonii*, which has the longest spadix in the genus, and in *C. stellasarreae*, which has one of the shortest. The sterile portion is also absent in some collections of *C. croatianae* subsp. *croatiana* and *C. dodsonii* and some spadices of *C. tokioensis*. In a few species, each portion of the spadix occupies approximately one third of the total length: *C. atropurpurea*, *C. castula*, *C. chocoensis*, *C. hastata*, and *C. mirabilis*. Although the sterile portion is shorter than the pistillate portion in all but one species of *Chlorospatha* (some collections of *C. atropurpurea*), it can be almost as long in the aforementioned species. In *C. hammeliana*, the fertile and sterile male portions are almost equal in length, as in the above species, but the pistillate portion is notably longer. The sterile portion is frequently longer than the fertile male portion and rarely longer than the pistillate portion in *C. atropurpurea*, apparently unique conditions in the genus.

The shape of the sterile portion is slightly variable on the species level, but is more or less cylindrical in most taxa and can be weakly broadest at either the base or apex in some species, occasionally either on different inflorescences in other species. The sterile flowers are either densely arranged or weakly coherent in most taxa, laxly arranged in 15 species, and can, in either case, but more frequently in the latter, have 1–2 mm or as much as half of the axis naked at the base of the sterile portion or with a few scattered flowers present in some taxa. In some species (e.g., *Chlorospatha grayumii*, *C. longiloba*, *C. sagittata*), the flowers can be densely arranged in one or more apical whorls and laxly arranged in the basal whorls, which is more frequently the case in species with more than one type of sterile flower on the same spadix. In *C. croatica* subsp. *croatica*, the flowers can be either laxly or densely arranged in one to six whorls or none may be present, depending on the collection, thus exhibiting the most variation in the genus. Flowers are arranged in five to as many as nine whorls in most *Chlorospatha* and in two to four whorls in 14 species, usually with a variation of one to two whorls or occasionally three whorls. The number of whorls is not correlated with the density of arrangement. *Chlorospatha stellasarreae* and *C. tokioensis* have flowers laxly and densely arranged respectively, in one to two whorls. Only three species can have flowers in more than nine whorls, *C. giraldoi* (eight to 10), *C. mirabilis* (seven to nine, or 11), and *C. noramurphyae* (12). In *Chlorospatha*, one or more sterile flowers frequently occur in the upper whorl of pistillate flowers, occasionally in one or two whorls immediately below the upper whorl.

The female portion of the spadix is narrow and usually cylindrical or ellipsoid, with the width equal to or slightly greater than that of the sterile portion. Even when the entire female portion is adnate to the spathe, it is subcylindrical, with most of the axis distinguishable and the flowers arranged around the exposed circumference, with one exception. In some collections of *Chlorospatha dodsonii*, the axis is obscure and appears to be imbedded in the spathe, with the flowers appearing to emerge directly from its inner surface and arranged in rows, thus rendering the pistillate portion much broader than thick. An intermediate condition was observed in some specimens of *C. besseae*, wherein the axis was weakly distinct from the spathe. The female portion is between 2 and 6 cm long in 41 taxa, as much as 6.7 cm long in *C. macphersonii*, 9 cm long in *C. dodsonii*, and can be less than 2 cm long in the remaining 22 species, consistently less in 12 of these, including *C. hannoniae*, *C. oblongifolia*, and *C. pubescens*, in

which this portion can be 7–8 mm long, the shortest in the genus. In all taxa, the diameter is usually more or less equal to that of the fertile male portion, but can be 2 mm greater in 10 species and 2–3 mm less in six species. In most *Chlorospatha*, the female portion is relatively densely flowered but never to the degree attributable to *Xanthosoma*, except in one collection of *C. mirabilis* (Croat & Mora 83686). In this collection, pistils in the central three fourths of the pistillate portion of the spadix are prismatic (viewed from above), and most of the length of each ovary is coherent with that of adjacent ovaries. In all other *Chlorospatha*, “densely arranged” pistils are better described as “weakly coherent,” meaning that some, but not all, portions of each ovary contact some portions of most or all adjacent ovaries. Excluding the aforementioned collection of *C. mirabilis*, the female portion is most densely flowered in *C. callejasii*, *C. cutucuensis*, *C. portillae*, and *C. sizemoreae*, but, as described above, the pistils are easily distinguishable as separate structures (with the naked eye) and not at all prismatic in appearance, which could not be said of members of *Xanthosoma*. In 16 species, the female flowers are more or less laxly arranged, with only a few or no ovaries weakly coherent, depending on the species, and the axis visible between most or all flowers in most species (see Female Flowers below). *Chlorospatha stellasarreae* is the most laxly flowered taxon, having only one to two pistils per whorl, with the whorls conspicuously remote from each other. The density of arrangement of the female flowers is consistent on the species level and taxonomically significant. In *Chlorospatha*, the female portion is typically more laxly flowered near and at the base, occasionally also in the apical one to two whorls in some species. The number of flowers across the axis, as described herein, refers to the number visible in face-view, essentially two-dimensionally, with the inflorescence intact, this number being applicable to all taxa, whether the spadix is fused to the spathe or not and, therefore, is more useful. This is described “as viewed from above” in this treatment. There are between three and five flowers across the axis in approximately half of all taxa, two to three flowers in 21 species, one to two flowers in one species (*C. stellasarreae*), and four to six flowers in seven taxa that have relatively large, densely flowered spadices. All species with laxly flowered spadices have less than four flowers across the axis, except those with relatively large spadices, e.g., *C. dodsonii*, *C. sagittata*.

Coloration of the female portion of the spadix is diverse in *Chlorospatha* but usually consistent on the species level in the 32 species in which color is

known. The color of the stylar region is frequently distinct from that of the sterile and fertile staminate portions. Although inflorescences of only a few species were examined, coloration of the pistillate portion apparently intensifies to some degree as the inflorescence develops toward anthesis, more conspicuously so than that of the fertile and sterile male portions. The female portion is white, cream-colored, or greenish to yellowish white or cream in nine taxa, but in two of these taxa it can also be pale yellow (*C. cutucuensis*) and pale yellow-green (*C. pubescens*). The female portion is pale to medium yellow, green, or yellow-green in nine species, more or less orange in three species, and purplish in two species. Other coloration is represented in single species: rose-colored in *C. besseae*, maroon in *C. sagittata*, red in *C. callejasii*, and pink in *C. hastata*. More variation was observed in three species, with the female portion white or yellow in *C. croatiana* subsp. *croatiana*, cream-colored, pale green, or yellow-green in *C. longiloba* and pink, pale yellow, or pale orange in *C. mirabilis*. Such diverse and more or less species-specific coloration of the female portion of the spadix would presumably serve some purpose in pollination.

Inflorescences of 19 species were examined at anthesis, 18 of which were pleasantly fragrant, with the fragrance fruity, sweet, spicy-sweet, spicy, mint-like, spicy-fruity, sweet-soapy, or like musty fruit that is beginning to rot, apparently reasonably consistent on the species level. Only one or several collections of each species were examined and the numbers of collections and examinations of each species were not sufficient to define the fragrance observed, but the fruity aspect appeared to be predominant. The perceptions of the various fragrances were subjective and, therefore, open to question, but certain general conclusions would appear to be useful, with the caveat that more careful research is needed. Fragrance began in early to mid-morning, as the spathe began to open, increased in intensity between noon and mid-afternoon, then decreased in late afternoon to early evening and was undetectable by nightfall of the first day of the flowering cycle. However, a weak fragrance of unknown origin was detected at the apex of the spathe on the second and third days in *Chlorospatha hannoniae*, *C. kolbii*, and *C. longipoda*. Madison (1978) maintained that the female flowers emitted the fragrance in *C. atropurpurea*, which does not appear to be the case. The spadices of *C. atropurpurea*, *C. croatiana* subsp. *croatiana*, *C. hannoniae*, *C. kolbii*, and *C. longipoda* were dissected into three portions, the fertile male, sterile male, and female portions, and the sterile male portion appeared to be the source of the fragrance.

The absence of fragrance in *C. plowmanii* cannot be explained. As in the other species observed, some of which are closely related, anthesis occurs during the day in this species, and the inflorescence was not fragrant during the night. It is possible that fragrance was present but not detectable by the observer. Since the species examined represent all known flowering strategies in the genus, it is likely that most *Chlorospatha* are fragrant and that fragrance serves an important function in pollination biology, coincidental with female anthesis.

Male flowers. The androecium of *Chlorospatha* consists of two to six stamens fused into a deeply or shallowly lobed synandrium, with the fused connectives thickened and the thecae extending almost to the base of the synandrium, opening by terminal pores or longitudinal slits (Madison, 1981; Mayo et al., 1997). In most taxa, the synandrium is more or less truncate at the apex, subprismatic, and more or less regularly polygonal (as viewed from above), although some elongation in the direction of the axis was observed in one to several whorls of the lowermost flowers in some taxa. In five species from the eastern slopes of the Andes in Ecuador, all synandria on the spadix were occasionally highly bilaterally symmetrical, usually moderately to prominently elongated in the direction of the axis and consistently broadly concave medially, with the margins of the lobes thickened, frequently accompanied by additional thickening around the individual pores, creating a more or less conspicuous tubelike effect: *C. boosii*, *C. hannoniae*, *C. longipoda*, *C. plowmanii*, and *C. pubescens*. In these species, the margins are prominently sinuate-undulate, interlocking with the margins of adjacent flowers, whereas those of typical synandria are only weakly to moderately sinuate and neither undulate nor interlocking.

Most synandria are 3- to 4-androus or 4-androus in more than 40 taxa and 3-androus in eight species. The number of stamens per flower is rarely constant on a single spadix, variation having been observed in all taxa except *Chlorospatha amalfiensis* with only three stamens and *C. munchiquensis* with only four stamens. Interestingly, on different spadices of *C. luteynii* and *C. mirabilis*, most synandria were either 3- or 4-androus, a condition not observed in other taxa. As many as five stamens were observed in 26 species, but frequently in only 11 of these species that usually had three to five stamens on a single spadix, with some synandria of *C. dodsonii* also having two stamens. Synandria with two to three stamens are found in only five species: *C. engleri*, *C. grayumii*, *C. oblongifolia*, *C. portillae*, and *C.*

sizemoreae, with those of *C. engleri* and *C. grayumii* occasionally having four stamens (on the same spadix). Otherwise, 2-androus synandria usually occur only occasionally near the base or apex of the fertile portion, occasionally also 1-androus synandria. Flowers with six stamens occur in only two species: *C. ricaurtensis* with (four)five to six, most of which have five; and *C. sagittata* with (three)four to six. The number of stamens in a synandrium is usually easily determined except in synandria that are not truncate at the apex, and occasional fusion of two adjacent synandria was observed in both forms of synandria, usually near the apex of the spadix. However, in some species, e.g., *C. engleri*, the synandria are so deeply lobed that individual stamens frequently appear to be separate, with the terminal pores relatively remote from each other, thus making the determination of the number of stamens more difficult. In most species, the synandrium is between 1 and 1.5 mm long, rarely less, and between 1 and 1.5 mm in diameter. Twenty-three taxa have synandria that can be 2–2.3 mm in diameter, with those of *C. ilensis* and *C. litensis* being as much as 2.5 mm in diameter and those of *C. dodsonii* as much as 3 mm in diameter, the largest known, commensurate with the large spadix of this species. Synandria can also be 2 mm long in *C. dodsonii*, *C. longiloba*, and *C. sagittata*. In some species, the synandria are somewhat elongated in the direction of the axis in the basal two to four whorls, and in *C. cutucuensis*, in all whorls in the basal half of the fertile portion. Elongation was most pronounced in *C. planadensis*, which has flowers 2 mm long and 1 mm wide (as viewed from above). Moderate to prominent elongation of all flowers on the spadix occurs in six species, *C. boosii*, *C. hannoniae*, *C. longipoda*, *C. plowmanii*, *C. pubescens*, and *C. ricaurtensis*, all members of *Chlorospatha* sect. *Orientalis* except *C. ricaurtensis*. In these six species, the synandrium, as viewed from above, is from 1.5 to 2.2 mm long, or to 2.5 mm long in *C. plowmanii*, and from 1 to 1.2 mm wide, or to as much as 1.5 mm wide in *C. pubescens*.

Sterile flowers. Sterile flowers in *Chlorospatha* are male flowers comprised of one or more staminodes that can be free or to some extent fused and branched, fungiform, or irregularly to evenly lobed. A “branched” flower consists of one to six staminodes that are fused only at or near the base and are otherwise free, with the individual branches clavate, ellipsoid or broadest at the apex and bluntly rounded, concave, truncate, or obtusely truncate, depending on the taxon. Red chromoplasts were observed in sterile flowers in some species, e.g., *C. croatianae* subsp. *croatiana*, *C. longipoda*. Although

the morphology of sterile flowers is remarkably diverse in *Chlorospatha*, it is reasonably consistent on the species level and taxonomically significant. Only evenly to irregularly lobed or subprismatic flowers occur in 42 taxa, occasionally as synandrodia in the apical whorl; eight taxa have some prismatic flowers in the apical one to three whorls. In *C. gentryi* and *C. yatacuensis*, the flowers are exclusively prismatic. All three types of flowers are more or less obpyramidal or somewhat anvil-shaped, and coherent the entire length of the sterile portion of the spadix in most taxa but are consistently laxly arranged the entire length in some species (e.g., *C. litensis*, *C. mirabilis*, *C. timbiquensis*), or only in the basal whorls (e.g., *C. grayumii*, *C. sagittata*). Synandrodia or irregularly lobed flowers also occur in the apical one to three whorls in most but not all remaining species in which most flowers are either branched or fungiform, or a combination of these. All or most of the sterile flowers are branched in eight species and in some collections of *C. kolbii*. In eight species, all or most of the sterile flowers are fungiform, with the flowers assuming one of three basic shapes, depending on the species. Two types of fungiform flowers resemble toadstools and are broadest at the apex and more or less abruptly narrowed below. In one of these two types, the broad apical portion is moderately to prominently convex, e.g., *C. kressii*, *C. longiloba*, *C. stellasarreae*, and *C. tokioensis*, and in the other type, moderately to prominently concave, e.g., *C. chocoensis*. The flowers of both types are usually more or less rounded or subprismatic when viewed from above, but in some species, can have moderately to conspicuously sinuate margins, e.g., *C. chocoensis* and *C. lehmannii*, and bear no resemblance to synandrodia. The third type of fungiform flower is found exclusively in three species, *C. atropurpurea*, *C. castula*, and *C. hastata*, and is irregularly and deeply cup-shaped, usually sessile, rarely weakly stipitate, with the medial concavity frequently extending almost to the base and the margins sinuate-undulate.

The remaining taxa have two types of sterile flowers prominently represented on the same spadix, each occurring on one third to two thirds of the sterile portion: *Chlorospatha caliensis*, *C. lehmannii*, *C. nambiensis*, and occasionally *C. kolbii*, with the latter having three different types of sterile flowers on some spadices, these being branched and fungiform toward the base, with synandrodia near the apex. The other three species have only branched and fungiform flowers on the same spadix. Considerable variation between different collections was observed in only one species, *C. croatianae* subsp. *croatiana*, wherein

the flowers were subprismatic, evenly or irregularly lobed, fungiform (either convex or concave at the apex), or branched, and either densely or laxly arranged, with the branches either clavate or obtusely truncate.

Regardless of shape, sterile flowers in *Chlorospatha* can be coherent, weakly coherent, laxly arranged, or any combination of these, but with the laxly arranged state confined to the portion toward the base if more or less coherent flowers occur on the same spadix. The density of arrangement of flowers is reasonably consistent on the species level. In 54 taxa, the flowers are approximately 1 mm long or less, most being 0.5–0.8 mm long or occasionally somewhat less. Five species can have flowers 1.5 mm long; those of *C. croatiana* subsp. *croatiana* can be 1.8 mm long; and *C. kolbii* and *C. lehmannii* can have the longest observed, as much as 2 mm long. The average diameter of flowers that are weakly or not at all elongated in the direction of the axis is 1–1.5 mm, but in four species, the diameter can be 2–2.2 mm and in five species, as little as 0.6–0.8 mm. Flowers are usually more or less elongated in the direction of the axis in most taxa, as viewed from above, and can be as much as 2–2.2 mm long and 0.6–1.5 mm wide in 20 taxa and 2.5–3 mm long in 14 species.

POLLEN

Chlorospatha pollen is extruded in strands as permanent tetrads, with the individual grains spheroidal or subspheroidal, inaperturate, apolar, radiosymmetric, and their limits frequently barely discernible, as circumscribed by Grayum (1992). However, Bogner (1997) observed that although the tetrads are usually arranged tetrahedrally in *Chlorospatha*, the pollen of *C. plowmanii* (= *Caladium plowmanii*) is shed in both tetrahedral and linear tetrads, based on his examination of SEM micrographs. Grayum considered inaperturate, globose, apolar, and radiosymmetric pollen to be the most advanced, which would include that of *Chlorospatha*. Individual grains have a mean diameter of 26 μm , with a range of 24 μm (*C. hammeliana*) to 29 μm (*C. castula*), and tetrads, a mean diameter of 40.5 μm , with a range of 33–48 μm . The pollen is, on average, more than 50% smaller than that of *Xanthosoma*, starchless and binucleate, whereas that of *Xanthosoma* is starchy and usually trinucleate (Grayum, 1986). Starchiness in pollen would appear to be directly correlated with pollen size and, therefore, the body size of the pollen vector. Starchless pollen stores energy in the form of lipids (as opposed to starch) that require more energy to produce and break down but

which are more compact and typically correlate with smaller pollen (Grayum, pers. comm.).

Grayum (1992) described the exine sculpturing of *Chlorospatha* as psilate and obscurely punctate (*C. corrugata*) to obscurely verruculate or, in *C. croatiana*, foveolate-reticulate with psilate bands marking the boundaries between grains and the foveolae as in certain species of *Dieffenbachia* Schott. Pollen from species not considered by Grayum was submitted by the authors, at the request of Josef Bogner, to Michael Hesse and Heidi Halbritter at Institut für Botanik der Universität in Vienna, Austria. The resulting micrographs indicate additional forms of exine sculpturing in *Chlorospatha*: reticulate in *C. hannoniae*, *C. plowmanii* (Fig. 3G–L, Croat & L. P. Hannon 81475), and *C. pubescens*; smooth (lacking ornamentation) in *C. dodsonii* (Fig. 2A–F, Croat et al. 82836) and *C. oblongifolia* (Fig. 3A–F, Croat & J. Gaskin 80957); or with unusual ornamentation circumscribed by Halbritter as “variable-perforated” in *C. kolbii* (Fig. 2G–L, Croat & Mora 83727). Additionally, Bogner observed the pollen of *C. kolbii* (Bogner s.n.) as irregularly reticulate to foveolate. Halbritter reported that the pollen of *C. atropurpurea* was peculiar in having holes in the walls (two collections examined).

FEMALE FLOWERS

Chlorospatha exhibits a variety of gynoecial characters that are taxonomically significant on the generic level, clearly distinguishing it from *Xanthosoma*, with each character exhibiting a range of diversity that is remarkable in some cases and usually consistent on the species level, thus providing an abundance of taxonomically useful and frequently diagnostic information. The female flowers are naked and unipistillate, lack staminodia, and can be either relatively densely or laxly arranged on the spadix (see Spadix, above). Pistils are 1.3–2 mm long in 31 taxa and 1.5–2 mm diameter in these and most remaining taxa, with the stylar region surrounding a central pollen tube canal and moderately to extremely short or elongated and more or less attenuated. In *C. jaramilloi*, *C. lehmannii*, and *C. noramurphyae*, pistils can be 2.5 mm long, and in *C. caliensis* and *C. dodsonii* as much as 3 mm and 3.2 mm long, respectively, the longest in the genus, with the stylar region comprising as much as two thirds of the total pistil length. *Chlorospatha dodsonii* is also one of eight species with pistils 2–2.5 mm in diameter, exceeded only by those of *C. noramurphyae* and *C. sagittata*, which are 2.5–3 mm in diameter. Fourteen species have pistils approximately 1 mm long or slightly less, with some pistils 0.6 mm long in *C.*

hannoniae and 0.5 mm long in *C. risaraldensis*, the shortest in the genus. The diameter of the pistil accords with the maximum diameter of the ovary in all but a few species in which the stylar region is conspicuously wider than the ovary (see Style and Stigma Morphology below).

Ovaries are more or less terete in cross-section, subglobose, or occasionally obtusely conical or ovoid, and weakly to deeply 2- to 4(5)-furrowed in the majority of taxa. Exclusively obtusely conical ovaries were observed only in *Chlorospatha dodsonii*, *C. jaramilloi*, *C. kressii*, and *C. sagittata*. It should be noted that numerous taxa are known only from dried material, which, owing to the delicate nature and small size of the female flowers, could possibly result in some misinterpretation of shape; however, we have applied knowledge of similar drying characteristics of flowers known from living material of other taxa in our interpretations of dried material. The shapes of mature ovaries on a spadix or different spadices of a given taxon are usually slightly variable in most taxa, depending on position on the spadix and density of arrangement or both, with proximal flowers usually less densely arranged and somewhat smaller than average, but more pronounced variation does occur. Subglobose and cylindrical or ovoid ovaries were observed on single spadices of *C. kolbii*, *C. macphersonii*, and *C. yatacuensis*. In the last two species, the cylindrical ovaries were approximately as long as wide or slightly wider than long, which is the typical condition in *Chlorospatha*, regardless of ovary shape. However, in *C. kolbii*, the ovaries (on some spadices) were more or less cylindrical to ovoid and longer than wide in the apical half of the pistillate portion of the spadix and subglobose in the basal half. Cylindrical to ellipsoid or ovoid ovaries are fairly common in *Chlorospatha* and usually representative of sectional differences (see Infrageneric Relationships). Cylindrical, ellipsoid, or ovoid ovaries that are longer than wide are found only in *Chlorospatha* sect. *Chlorospatha*, with two exceptions, *C. cutucuensis* and *C. portillae*, members of section *Orientales*. The pistils in most taxa in section *Chlorospatha* are relatively densely arranged, with those of *C. mirabilis* being the most densely arranged and described by Masters (1874) as subcuboidal, reflecting the obtuse angularity commensurate with this arrangement. The cylindrical ovaries found in other species are usually dimensionally typical except in eight of the 10 species assigned to *Chlorospatha* sect. *Orientales*, in which ovaries are approximately 1 mm long or less, frequently 1.5 to 2 times wider than long, and frequently more or less broadly concave at the apex, whereas typical ovaries are more or less rounded or

obtusely truncate at the apex and about as wide as long. Obtusely obconical ovaries frequently occur exclusively or in conjunction with cylindrical ovaries on the same spadix in these eight species in section *Orientales*. Only in these species and one collection of *C. mirabilis* (Croat & Mora 83686) is the ovary as broad as or broader at or near the apex than at the base, the ovary in *Chlorospatha* typically being weakly to prominently narrower at the apex, regardless of shape.

The coloration of ovaries is presumably the same or similar to that of the axis and is white, cream, or somewhat greenish in most taxa. In *Chlorospatha sagittata*, the axis is dark maroon and the ovaries so densely dark maroon-speckled that these also appear to be entirely dark maroon. The axis in *C. kressii* is dark violet, but the coloration of the ovaries is not known. Atypical coloration was observed in two collections. In Croat 74799 (*C. croatiana* subsp. *croatiana*), the axis is white and the ovaries are lavender-tinged white, with dark purple streaks toward and at the base. Similar coloration was observed in Hort. Veitch s.n. (*C. mirabilis*).

The internal morphology of the ovary and most or all of its attendant parts are known in 23 floristically diverse species in which most or possibly all morphological conditions in the genus are probably represented. There are (one) two to four (five to six) locules in ovaries of *Chlorospatha*, with the locules usually ovoid or somewhat spherical, or subspherical and slightly wider than long, and the septa exceedingly thin and translucent or almost as thick as the ovary walls, depending on the species. Locules in all taxa examined extended most of the length of the ovary and contained no fluid. The number of locules present in ovaries on a given spadix varies within a reasonably consistent range on the species level, with the ovaries usually or consistently 2-locular in nine species, consistently 2- to 3-locular in seven species, usually or consistently 3- to 4-locular in five species, and consistently 3-locular in three species. Species that usually or consistently have 2-locular ovaries are known from both slopes of the Andes in Ecuador, with five of the six species from the eastern slopes being the only species of *Chlorospatha* known usually to have some 1-locular ovaries: *C. boosii*, *C. hannoniae*, *C. limonensis*, *C. plowmanii*, and *C. pubescens*. In *C. boosii*, *C. hannoniae*, *C. limonensis*, *C. pubescens*, and most collections of *C. plowmanii*, 1-locular ovaries were observed almost exclusively in the basal whorls, rarely immediately above the basal whorls in the basal half of the pistillate portion of the spadix. The condition is clearly pseudomonomerous, the ovaries

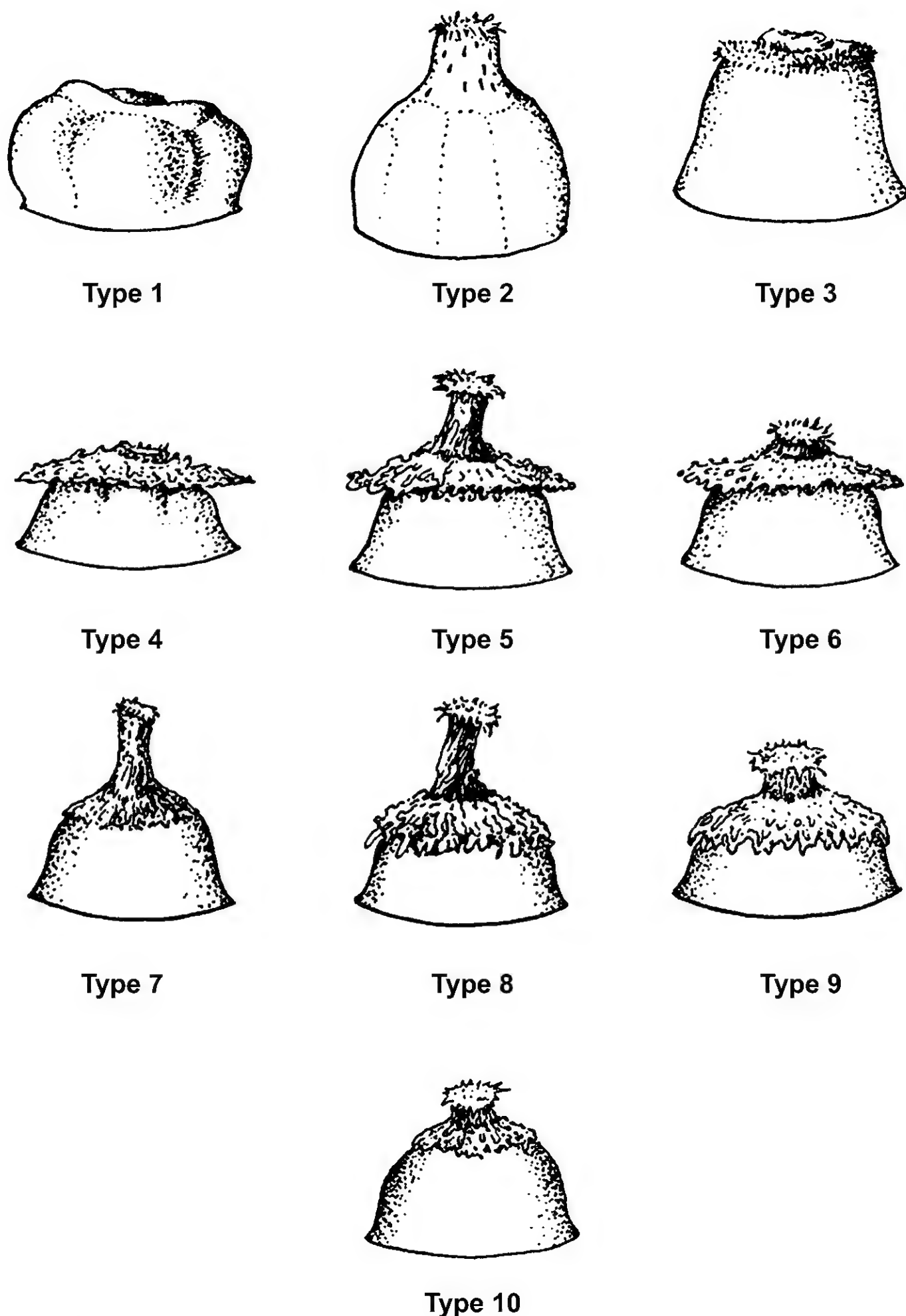


Figure 1. *Chlorospatha* style types 1–10. [Style types were created from a collective set of specimens from species that encompass an entire styler group, no one singular species.] —Type 1. Styles not or obscurely attenuate, less than 1/4 the pistil length, and lacks a mantle, as seen in eight species of *Chlorospatha* Engl. sect. *Orientalis* Croat & L. P. Hannon (e.g., *C. boosii* Croat & L. P. Hannon). Style Type 1 ranges from 1 to 2 mm diam. —Type 2. Styles shortly attenuate, 1/4 to 1/3 the pistil length, and lacks a mantle, as in three species of *Chlorospatha* sect. *Orientalis* (e.g., *C. cutucuensis* Madison). Style Type 2 ranges from 0.8 to 1 mm diam. —Type 3. Styles only obscurely attenuate, to 1/4 or less the pistil length, expanded in a disklike mantle as wide as the ovary apex, as seen in *Chlorospatha* sect. *Chlorospatha* as seen in 18 taxa (e.g., *C. betancurii* Croat & L. P. Hannon). Style Type 3 ranges from 0.75 to 2 mm diam. —Type 4. Styles obscurely or not attenuate, significantly less than 1/4 of the pistil length, with an obvious mantle much wider than the ovary apex, as in four species in *Chlorospatha* sect. *Occidentales* Croat & L. P. Hannon (e.g., *C. Castula* (Madison) Madison). Style Type 4 ranges from 1 to 3 mm diam. —Type 5. Styles long attenuate and ca. half the pistil length, the style broadly expanded into a mantle much wider at the base than the ovary apex, found in six species in *Chlorospatha* sect. *Occidentales* (e.g., *C. grayumii* Croat & L. P. Hannon). Style Type 5 ranges from 1.2 to 2.6 mm diam.

being multicarpellate in all cases, with multiple furrows and frequently the vestiges of one to two septa present. In *C. boosii* and *C. hannoniae*, which flower seasonally, more 1-locular ovaries were observed (in cultivation), with the ovules depauperate, toward the end of the flowering season, when the plants were flowering less vigorously. The type of *C. plowmanii* (Plowman et al. 3979) is the exception, having most or possibly all ovaries unilocular. All ovaries of this collection were not dissected, but several were examined at different positions along the length of the pistillate portion and found to be unilocular. In an apparently aberrant collection tentatively assigned to *C. longipoda* (Croat et al. 86607), most ovaries were 2-locular, but many, at various positions on the spadix, were 1-locular with markedly depauperate ovules and vestigial septa present in some ovaries (at first flowering in cultivation). However, the spathe blade remains erect after anthesis in this collection, unlike that in all collections of *C. plowmanii*, which reflexes after anthesis. Placentation was basal in the 1-locular ovaries in this collection, a condition found only in the type of *C. plowmanii* (and in *C. castula*). Madison (1978) reported a semi-unilocular condition in *C. atropurpurea* and *C. castula*, describing the ovaries of *C. atropurpurea* as 3- to 4-locular near the base, with the parietal placentae axially connate and deeply intrusive, with axile placentation becoming unilocular near the apex. Earlier, Madison (1976) described the ovary of this species as 2- to 3-locular with axile placentation, but with the septa weakly united in the center and frequently separating, thus appearing as two to three deeply intrusive parietal placentae (“as in *Caladium*”). The ovaries of three living collections of *C. atropurpurea* were examined by the authors and found to be 2- to 4-locular, with the septa connate the entire length and placentation axile, with no indication of a unilocular condition near the apex. However, all of the collections examined were from Esmeraldas Province, Ecuador, and the type is from Los Ríos Province, farther to the south. It is likely that this is the collection Madison examined, and perhaps the geography involved can

entirely, or in part, explain this discrepancy, since this condition is possibly variable. Madison (1981) described the ovary of *C. castula* as tricarpellate and semi-unilocular, with the unilocular condition occurring at the apex. Neither fresh nor pickled material of this species was available for examination.

The Hort. Veitch s.n. collection of *Chlorospatha mirabilis* is the only collection of *Chlorospatha* reported to have more than 4-locular ovaries, with a handwritten note on the label reporting the presence of three to six locules. However, a maximum number of four locules was observed (by the authors) in ovaries of a living collection of this species and Masters (1874) described the ovaries as 4-locular; therefore, 4- or 6-locular ovaries would be unique in the genus. Mayo et al. (1997) describe the berries of *Chlorospatha* as 3- to 5-furrowed, indicating the presence of as many as five carpels; however, the authors have observed no more than 4-furrowed ovaries or berries. Only one living collection of *C. mirabilis* could be examined, and it is hoped that the examination of additional collections will clarify this issue.

Ovules. The 23 species in which the number of ovules per locule (in plurilocular ovaries) was determined or estimated (*Chlorospatha lehmannii*) usually had between six and 10 ovules in each locule, with species occasionally having three or four, and six species consistently having more numerous ovules. Two species consistently had relatively few ovules, *C. atropurpurea* with three to seven per locule and *C. hastata* with four to eight per locule. Locules of *C. ilensis* and *C. longipoda* frequently have 12 ovules and those of *C. dodsonii*, *C. engleri*, *C. longiloba*, and *C. sizemoreae*, 14 ovules. The few unilocular ovaries in species that otherwise have plurilocular ovaries usually have 10 to 16 ovules, with those of *C. boosii* having only eight and those of *C. hannoniae* and *C. plowmanii* as many as 20. Ovules are usually approximately 0.15–0.22 mm in length, with the funicles as long as the ovules in three species, longer than the ovules in six species, and shorter than the ovules in 13 species,

←

—Type 6. Styles briefly attenuate and ca. 1/3 of the pistil length, the style broadly expanded into a mantle wider than the ovary apex, as seen in two species in *Chlorospatha* sect. *Occidentales* (e.g., *C. antioquiensis* Croat & L. P. Hannon). Style Type 6 ranges from 0.6 to 2 mm diam. —Type 7. Styles long attenuate and 1/2 to 2/3 of the pistil length, the style expanded into a spreading mantle approximate to or narrower at the base than the ovary apex, observed in three species in *Chlorospatha* sect. *Occidentales* (e.g., *C. caliensis* Croat & L. P. Hannon). Style Type 7 ranges from 0.3 to 1.5 mm diam. —Type 8. Styles long attenuate and 1/2 to 2/3 of the pistil length, the stilar mantles not or weakly coherent, and confined to seven species in *Chlorospatha* sect. *Occidentales* (e.g., *C. amalfiensis* Croat & L. P. Hannon). Style Type 8 ranges from 0.7 to 2 mm diam. —Type 9. Styles briefly attenuate and ca. 1/3 of the pistil length, the stilar margins coherent or weakly coherent (nine species) or not coherent (*C. bayae* Croat & L. P. Hannon), and seen in *Chlorospatha* sect. *Occidentales* (e.g., *C. bayae*). Style Type 9 ranges from 0.8 to 2 mm diam. —Type 10. Styles briefly attenuate, usually 1/4(to 1/3) of the pistil length, the stilar margins not coherent, and restricted to four species in *Chlorospatha* sect. *Occidentales* (e.g., *C. congensis* Croat & L. P. Hannon). Style Type 10 ranges from 0.7 to 5 mm diam.

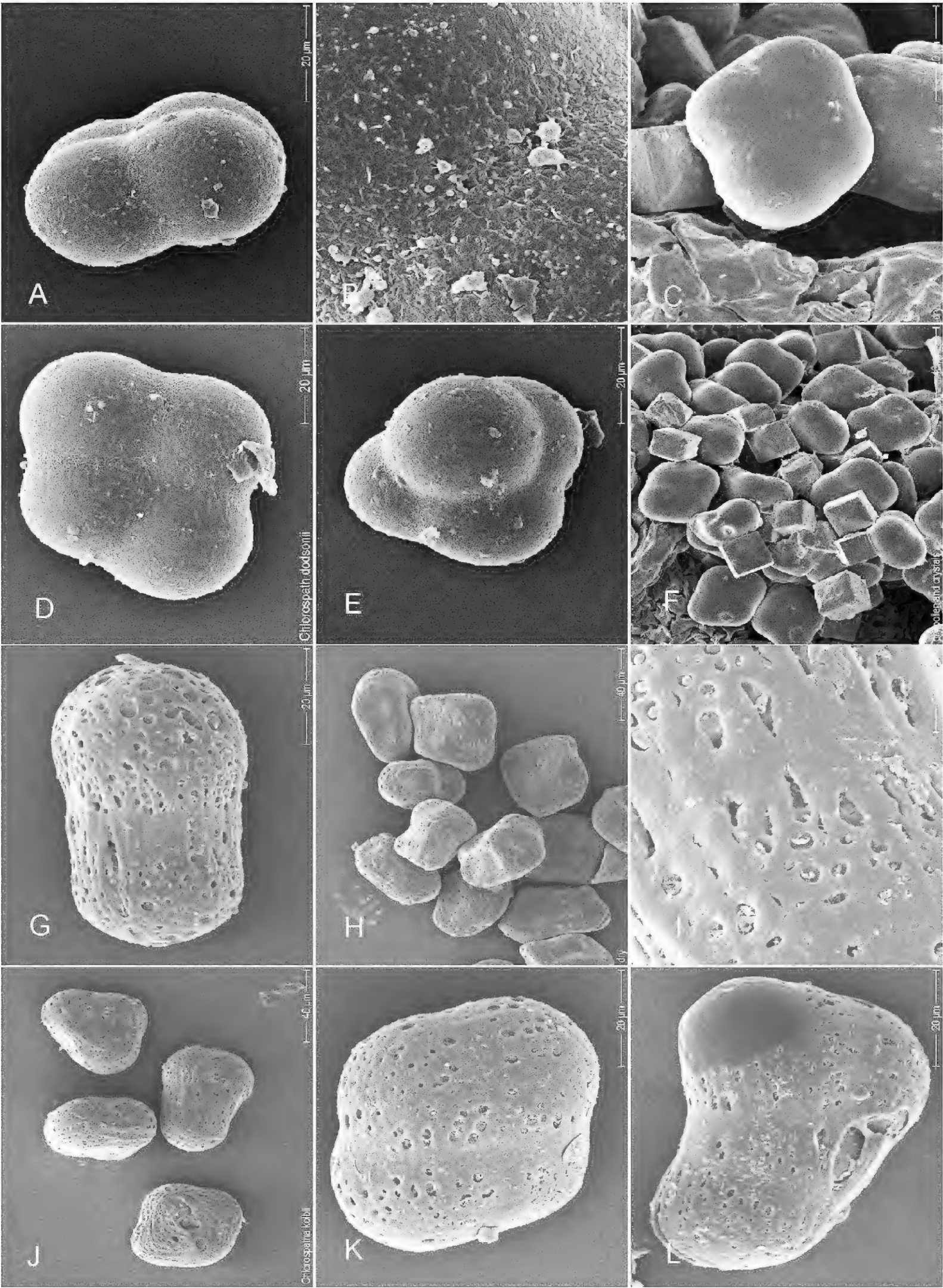


Figure 2. A–F. *Chlorospatha dodsonii* (G. S. Bunting) Madison, Croat *et al.* 82836 (MO). —A. Pollen tetrad, side view. —B. Close-up of tetrad surface. —C. Close-up of tetrad (center). —D. Tetrad, top view. —E. Tetrad, oblique view. —F. Tetrads interspersed with crystals. G–L. *Chlorospatha kolbii* Engl., Croat & Mora 83727 (COL, MO). —G. Tetrad, side view. —H. Group of pollen tetrads. —I. Close-up of tetrad surface. —J. Tetrads, top view. —K. Tetrad, top view. —L. Tetrad, oblique view.

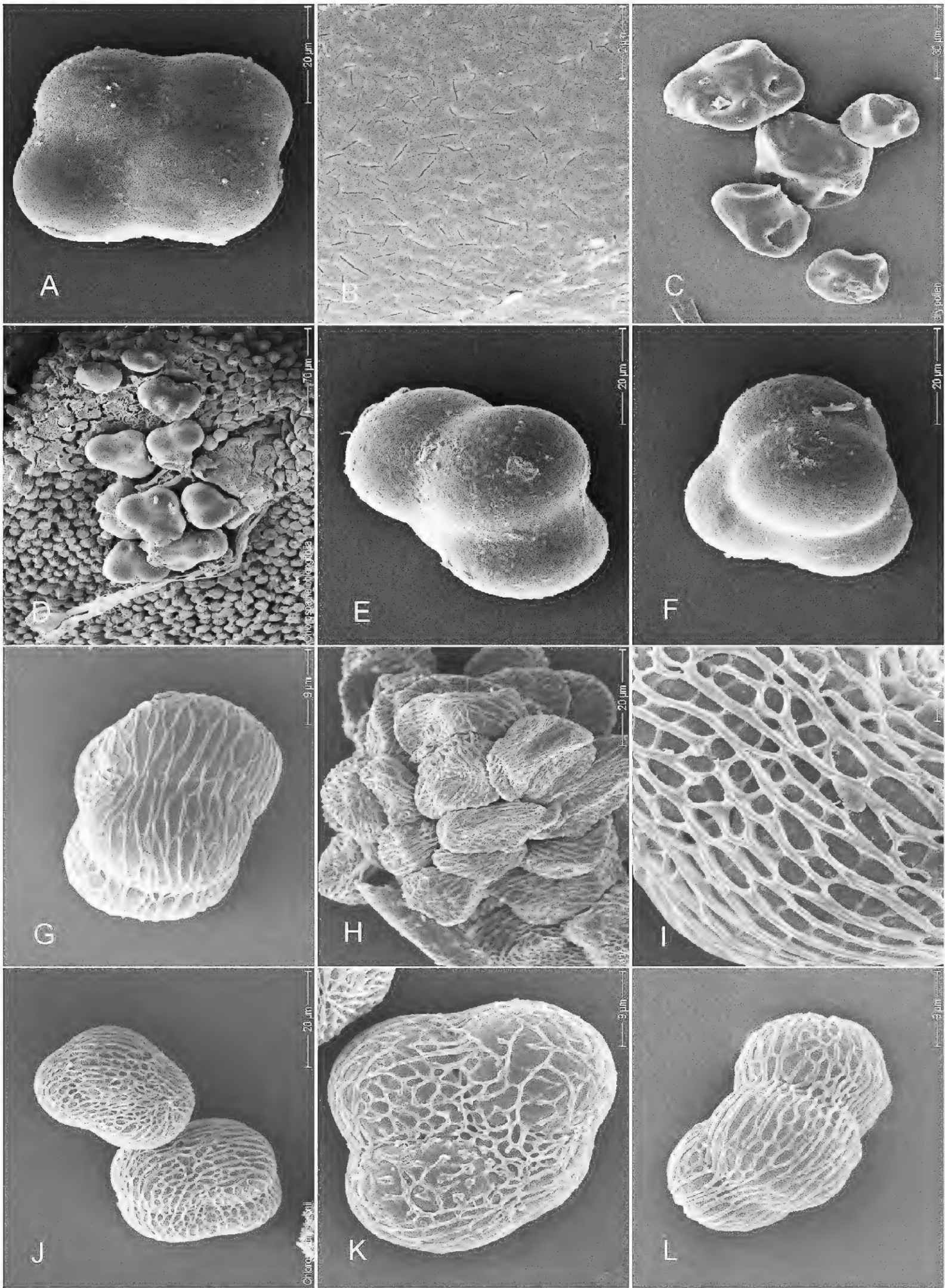


Figure 3. A–F. *Chlorospatha oblongifolia* Croat & L. P. Hannon, *Croat & Gaskin 80957* (MO). —A. Pollen tetrad, top view. —B. Close-up of tetrad surface. —C. Group of tetrads. —D. Group of tetrads emerging from anther. —E. Tetrad, side view. —F. Tetrad, oblique view. G–L. *Chlorospatha plowmanii* (Madison) Croat & L. P. Hannon, *Croat & L. P. Hannon 81475* (MO). —G. Tetrad, side view. —H. Group of tetrads. —I. Close-up of tetrad surface. —J. Tetrad, oblique view. —K. Tetrad, top view. —L. Tetrad, side view.

except in *C. croatian* subsp. *croatiana*, in which these can also be longer. All eight species from the eastern slopes of the Andes for which funicle length is known have funicles shorter than the ovules.

Ovules are anatropous or hemianatropous in *Chlorospatha*. Of the 23 species from both slopes of the Andes for which ovule orientation was determined, 17 had hemianatropous ovules. Anatropous ovules were observed in *C. hastata*, *C. kolbii*, and *C. oblongifolia* from the western slopes and *C. cutucuensis*, *C. longipoda*, and *C. sizemoreae* from the eastern slopes. Most ovules are more or less subhemispherical in longitudinal section, but the ovules were dorsiventrally compressed and comparatively narrow in one collection of *C. corrugata* (E. Spear s.n.), two collections of *C. croatian* subsp. *croatiana* (Croat & Grayum 60208, Croat 74799), and one collection of *C. longipoda* (Croat 59100). Other collections of *C. longipoda* had what are presumably typically shaped ovules. Ovule orientation in *C. corrugata* and *C. mirabilis* was determined from illustrations in Mayo et al. (1997) and Masters (1874), respectively.

The embryology of *Chlorospatha* has, to our knowledge, not been examined. However, according to Grayum's (1991b) treatment of embryology, the ovules would presumably be bitegmic in *Chlorospatha*, with the inner integument forming the micropyle, this being the typical condition in Araceae, unitegmic ovules having been reported only in *Montrichardia* Crueg.

Placentation. Placentation is pseudoaxile, axile, subaxile, or rarely sub-basal or basal in *Chlorospatha*. Pseudoaxile placentation, as defined by Mayo et al. (1997), is "a form of parietal placentation in which the placentae are borne on very deeply intrusive partial septa which may be partially fused (e.g., basally or apically)." Pseudoaxile placentation was observed in eight species. Superficially, the placentae appear to be a single axis, with placentation effectively axile or subaxile, with ovules occurring the entire length and placentation axile in *C. atropurpurea*, *C. lehmannii*, *C. plowmanii*, and *C. sagittata*; occurring only on the basal two thirds and placentation subaxile in *C. cutucuensis* and *C. kolbii*; or occurring the entire length and axile or on the basal one half to two thirds and subaxile in *C. longipoda*. Madison's descriptions of the ovaries of *C. castula* (1981) and *C. atropurpurea* (1976, 1978) clearly indicate a pseudoaxile condition. However, three collections of *C. atropurpurea* examined by the authors had true axile placentation, with the septa connate the entire length. In *C. castula*, placentation is effectively basal, according to Madison's descrip-

tion, a rare condition observed only in the type collection of *C. plowmanii* and some ovaries of an aberrant collection of *C. longipoda* (Croat 86607). Excluding the aforementioned species, true axile and subaxile placentation were the most common states observed in *Chlorospatha*, with placentation axile in 10 species, subaxile in four species, and either axile or subaxile in one species, *C. boosii*, one of the six species examined that usually have 2-locular and occasionally some 1-locular ovaries, the others being *C. hannoniae*, *C. limonensis*, *C. longipoda*, *C. plowmanii*, and *C. pubescens*. In the species not previously discussed, 1-locular ovaries (when present) have an interrupted axis in *C. hannoniae*, *C. limonensis*, and *C. pubescens*, whereas those of *C. boosii* have a complete, but extremely thin, fragile axis, and all but *C. hannoniae* have subaxile placentation. Unilocular ovaries of *C. hannoniae* have a sub-basal placental ring with depauperate ovaries arranged in a single row along the margin.

Arrangement of the ovules was consistently biseriate in 16 of the 23 species in which the condition could be determined. Placentae were 1- to 2-seriate in *Chlorospatha croatian* subsp. *croatiana*, *C. longipoda*, and possibly other taxa. It is possible that what would appear to be uniseriate placentae in *Chlorospatha* are actually biseriate, with the funicles attached alternately along the placental ridge, a condition that Mayo (1989) maintained might occur in apparently uniseriate placentae in *Philodendron*. This could not be determined in *Chlorospatha*, the arrangement of ovules in uniseriate placentae being somewhat disorganized in most cases. In *C. hannoniae*, *C. limonensis*, and *C. oblongifolia*, placentae were usually biseriate, but occasionally also 3-seriate. Engler (1920) described the ovules of *C. lehmannii* as biseriate, but his illustration of the ovary in this species indicates a 3- to 4-seriate condition.

Style and stigma morphology. **Style Type 1** (Fig. 1) lacks a mantle and is weakly thickened, comprising significantly less than one fourth of the length of the pistil, as broad as or somewhat narrower than the ovary apex, more or less truncate at the apex, and occasionally broadly concave medially. Though usually not attenuated, it can rarely be obscurely so. Style Type 1 is restricted to eight species in *Chlorospatha* sect. *Orientales*, from the eastern slopes of the Andes in Ecuador, and is the predominant style type in the region: *C. boosii*, *C. engleri*, *C. hannoniae*, *C. limonensis*, *C. longipoda*, *C. plowmanii*, *C. pubescens*, and *C. yaupiensis*.

Style Type 2 (Fig. 1) lacks a mantle and is similar to Style Type 1, but differs in being briefly to

moderately attenuated, thus comprising one fourth to one third of the length of the pistil. Style Type 2 is restricted to three species from the eastern slopes of the Andes in Ecuador, *Chlorospatha cutucuensis*, *C. portillae*, and *C. sizemoreae*, members of *Chlorospatha* sect. *Orientales*. In a pickled inflorescence of *C. cutucuensis*, the style appeared to be somewhat elastic, being prominently and variably wrinkled on some pistils, particularly at the apex, frequently forming a “collar” around the stigma, with only the apex of the stigma visible above the apex of the style. Fresh material of this species was not examined. This condition does not appear to occur in *C. portillae* or *C. sizemoreae*.

Style Type 3 (Fig. 1) is expanded into a disklike mantle that is approximately as wide as the ovary apex and surrounds the stigma, thus obscuring its point of attachment. The style is not typically attenuated, but can rarely be obscurely so, and comprises one fourth or less of the length of the pistil. Style Type 3 is confined to taxa in *Chlorospatha* sect. *Chlorospatha*, which is comprised of all taxa (18) that consistently or occasionally have divided leaf blades, with one exception, *C. corrugata*, a species with divided blades and Style Type 4 (Fig. 1). All taxa with Type 3 styles occur in Central America or northern Colombia, except *C. ilensis*, which is from Ecuador.

Style Type 4 (Fig. 1) is expanded into a broadly spreading mantle much wider than the ovary apex, obscuring the point of attachment of the stigma, and is obscurely or not at all attenuated. Style Type 4 comprises ca. one fourth or less of the length of the pistil and is confined to four species in *Chlorospatha* sect. *Occidentales*. *Chlorospatha corrugata* occurs only in northern Colombia. The other three species, all from the western slopes of the Andes in Ecuador, exhibit some noteworthy variation. In *C. castula* and *C. hastata*, the mantle is extremely thin, composed of tuberculate cells and is as much as 3 times wider than the ovary apex, with the margins more or less coherent with those of adjacent mantles. The mantle of *C. corrugata* is similar to that of these two species. The mantle in *C. sagittata* is not as broadly spreading and is slightly thicker, composed of subhemispherical cells, and the margins usually are not coherent with those of adjacent mantles.

Style Type 5 (Fig. 1) is expanded into a broadly spreading mantle that is conspicuously wider at the base than the ovary apex and not appressed to the ovary. The long-attenuated style comprises approximately one half of the length of the pistil, with the margins of the mantles more or less coherent or weakly coherent with those of adjacent mantles. Style

Type 5 is restricted to six species in *Chlorospatha* sect. *Occidentales*: *C. grayumii*, *C. huilensis*, *C. jaramilloi*, *C. longiloba*, *C. narinoensis*, and *C. planadensis*. Five of these species occur only on the western slopes of the Andes in Colombia and Ecuador. Some collections of the sixth species, *C. huilensis*, were made in the Magdalena River drainage on the western slopes of the Cordillera Oriental in Colombia; however, one or possibly two collections were made in the Amazon drainage, at the southern terminus of the mountain range. This species and *C. sucumbensis* (Style Type 9, Fig. 1) from northern Ecuador are the only species occurring in the Amazon drainage that have styles expanded into mantles. Some dried material of this style type could possibly be confused with Style Type 8 (Fig. 1H), regarding whether the mantle is appressed to the ovary; however, the distinction is clear in living or pickled material.

Style Type 6 (Fig. 1) is expanded into a broadly spreading mantle that is conspicuously wider at the base than the ovary apex and not appressed to the ovary. The briefly attenuated style comprises approximately one third of the length of the pistil, with the margins of all mantles more or less coherent or weakly coherent. Style Type 6 is restricted to two species in *Chlorospatha* sect. *Occidentales*: *C. antioquiensis* from the Magdalena River drainage in Colombia and *C. litensis* from northern Ecuador. Some dried material of this style type could possibly be confused with Style Type 9 (Fig. 1), regarding whether the mantle is appressed to the ovary; however, the distinction is clear in living or pickled material.

Style Type 7 (Fig. 1) is expanded into a spreading mantle approximately as wide as or slightly wider or narrower at the base than the ovary apex. The long-attenuated style comprises one half to two thirds of the length of the pistil, with the margins of the mantles not at all coherent in two species and weakly coherent in one species (*Chlorospatha caliensis*). Style Type 7 is restricted to three species known only from dried material, in *Chlorospatha* sect. *Occidentales*: *C. caliensis*, *C. lehmannii*, and *C. stellasarrae*, from the western slopes of the Andes in Colombia.

Style Type 8 (Fig. 1) is expanded into a spreading mantle that is appressed to the ovary and slightly wider at the base than the ovary apex. The style is long-attenuated and comprises one half to two thirds of the length of the pistil, depending on the species. The margins of the mantles are not at all coherent in five species and somewhat weakly coherent in two species. Some dried material of this style type could possibly be confused with Style Type 5 (Fig. 1), but

style type is easily determined in living or pickled material. Style Type 8 is confined to seven species from the western slopes of the Andes in Colombia and Ecuador and the Magdalena River drainage in Colombia, all members of *Chlorospatha* sect. *Occidentales*: *C. amalfiensis*, *C. atropurpurea*, *C. dodsonii*, *C. giraldoi*, *C. nambiensis*, *C. noramurphyae*, and *C. tokioensis*.

Style Type 9 (Fig. 1) is expanded into a spreading mantle that is appressed to the ovary and weakly wider at the base than the ovary apex. The style is briefly attenuated and comprises approximately one third of the length of the pistil. The margins of mantles are coherent or weakly coherent in nine species and not at all coherent in one species (*Chlorospatha bayae*). Some dried material of this style type could possibly be confused with Style Type 6 (Fig. 1), but style type is easily determined in living or pickled material. This style type is confined to 10 species from the western slopes of the Andes in Colombia and Ecuador, all members of *Chlorospatha* sect. *Occidentales*: *C. bayae*, *C. besseae*, *C. bogneri*, *C. bullata*, *C. carchiensis*, *C. mansellii*, *C. ricaurtensis*, *C. sucumbensis*, *C. timbiquensis*, and *C. yatacuensis*.

Style Type 10 (Fig. 1) is expanded into a spreading mantle that is approximately as wide as or weakly wider or narrower at the base than the ovary apex. The style is briefly attenuated and comprises approximately one fourth to one third (usually one fourth) of the length of the pistil, with the margins of the mantles not at all coherent. Style Type 10 is restricted to four species from the eastern and western slopes of the Cordillera Occidental in Colombia, all members of *Chlorospatha* sect. *Occidentales*: *C. congensis*, *C. macphersonii*, *C. nicolsonii*, and *C. oblongifolia*.

The stylar region in *Chlorospatha* is herein defined as that portion of the gynoecium between the ovary locules and stigmatic epidermis, with the terminology attributed to Mayo et al. (1997), who rightly note that the “style” can be as broad as the ovary and not elongated or attenuated in some Araceae, which is clearly the case in approximately 40% of taxa of *Chlorospatha*. However, for the sake of simplicity and in consideration of the fact that a distinct stylar region exists in all *Chlorospatha*, the term “style” will henceforth be used in descriptions and discussions. Fresh or dried styles exhibit considerable diversity of form, even when viewed with a hand lens (10×). The various forms are frequently critical in delimitation of species and easily distinguishable in fresh material, although some morphological details are visible only microscopically, after dissection. In all taxa, the main body of the style is distinguished from the ovary,

externally, by a visible (30×) rimlike margin at the base of the style, although this margin can be somewhat obscure in some species (see Style Types 1 and 2, Fig. 1). Mantles, when present, must be removed in order to expose this margin. The diameter at the base of the main body of the style is the same as or somewhat narrower than that of the ovary apex.

Stylar morphology in *Chlorospatha* falls into two general but distinct categories herein designated, to facilitate reference in this discussion, as Category A, represented by 60 taxa with the style expanded into a mantle that is apparently, for the most part, not fused to the main body of the style (Style Types 3–10), and Category B, represented by 11 species in which the mantle is lacking (Style Types 1 and 2). Style Types are illustrated in Figure 1. Taxa with styles in Category A are further divided into two groups that reflect sectional differences: *Chlorospatha* sect. *Chlorospatha* and *Chlorospatha* sect. *Occidentales* (see Infrageneric Relationships above). In *Chlorospatha* sect. *Chlorospatha*, the style is obscurely or not at all attenuated or elongated and the mantle is more or less disklike, approximately as broad as or weakly narrower or broader than the ovary apex and usually less than 0.5 mm long, comprising a small fraction of the length of the pistil. The mantle surrounds the stigma, obscuring its point of attachment; therefore, the stigma appears to be sessile in all taxa in this section. The stigma is indeed sessile in *C. kolbii* (lacking any obvious style) and presumably so in other taxa in this section; however, dissection of the living pistils of some collections of *C. croatiana* subsp. *croatiana* and *C. ilensis* revealed an obscure attenuation of the style that could possibly occur in other taxa. The styles in all taxa belonging to *Chlorospatha* sect. *Chlorospatha* are Type 3 (Fig. 1), which occurs exclusively in this section.

In *Chlorospatha* sect. *Occidentales*, comprised of the second group of taxa in Category A, the style is typically more or less attenuated, comprising one fourth to two thirds of the length of the pistil, with the stigma elevated on the narrowed portion, rarely sessile or apparently so, and the mantle either spreading or appressed to the ovary and weakly to prominently broader than or as broad as the ovary apex. The mantle surrounds the entire length of the main body of the style subtending the stigma and terminates at its apex. Diversity of form is highest in this section, with seven of the 10 style types observed in *Chlorospatha* represented. Characters that separately or in combination delimit the style types in this section, in order of significance, are: the ratio of the length of the style to that of the pistil; whether the mantle is spreading or appressed to the ovary and, if

spreading, whether it is as wide as or slightly to moderately or distinctly wider than the ovary apex; and the degree to which the margins are coherent (or not) with those of adjacent styles. These characters and their various combinations are remarkably consistent on the species level, even in relatively wide-ranging taxa in which one might expect more variation. The style occupies one half or slightly more of the length of the pistil in 15 species, one third of the length in 12 species, one fourth to one third of the length in four species, and two thirds of the length in two species, and is atypical in four species in which the style occupies significantly less than one fourth of the length of the pistil: *C. castula*, *C. corrugata*, *C. hastata*, and *C. sagittata* (Style Type 4, Fig. 1). Madison (1978) maintained that the stigma of *C. castula* is sessile; however, it is possible that its stylar morphology accords with that of *C. hastata* and *C. sagittata* in which the style is obscurely attenuated, with the mantle obscuring the point of attachment of the stigma, thus rendering the stigma only apparently sessile (as observed in dissected living material). Therefore, the style of *C. corrugata* is possibly also obscurely attenuated.

The style is between 0.5 and 1.2 mm long in most species in *Chlorospatha* sect. *Occidentales*, but can be 2 mm long in *C. caliensis* and *C. dodsonii*, occupying two thirds of the total pistil length, and as little as 0.3–0.5 mm long in *C. oblongifolia*, *C. stellasarreae*, and *C. yatacuensis*, which have small pistils with styles occupying between one fourth and one half of the total pistil length, depending on the species. The ratio of the length of the style to the length of the pistil correlates with style type and, therefore, is a more taxonomically significant character than the actual length of the style, which varies considerably in *Chlorospatha*, according to the size of the flowers. The same principle would apply to the diameter. The diameter of the style is 1–1.3 mm in some species with relatively short pistils and styles either broader or narrower than the ovary apex; therefore, the relative diameter is more significant than the measured diameter. In most taxa, the diameter of the style is between 1.5 and 2.3 mm, but exceeds this in five species with styles 2.5–2.6 mm in diameter and in *C. castula* with the style 3 mm in diameter. The diameter of the style, as given in descriptions of taxa that possess a mantle, refers to the maximum diameter of the mantle (at the base) rather than to that of the main body of the style beneath it and is the taxonomically significant character. Similarly, the length of the style, as applied in descriptions, refers to the length from the apex to the base of the mantle, which in species

with the mantle appressed to the ovary, can be greater than the length of the main body of the style, the base of which is obscured by the mantle.

In both aforementioned groups, the mantle can consist of one to two layers of hyaline or subspherical cells (Madison, 1978), or tuberculate cells, with few to numerous red chromoplasts visible in some taxa. Red chromoplasts were not observed, but possibly occur in the main body of the style beneath the mantle. In most taxa, the mantle lacks structural integrity, the cells being easily separated and the mantle itself easily scraped away in an amorphous mass. However, mantles comprised of subspherical cells, in some Type 4 and Type 3 styles and most Type 8 and Type 9 (see Fig. 1) styles, can be easily lifted off more or less intact (in living material but not pickled material), the cells not being easily separated.

The youngest inflorescences in sympodia were dissected in order to determine whether the mantle was excreted at some point in its development. The mantle was present in all dissections, which were performed at various stages of development and revealed no change other than an increase in size and moderate increase in color value as inflorescences matured. Therefore, though the mantle is not entirely fused to the main body of the style, it is integral with it. It would appear that the mantle is not homologous to the discoid style of *Xanthosoma*, since it represents only a portion of the style in *Chlorospatha* and is neither similarly fused to the ovary nor typically entirely coherent with adjacent styles as it is in *Xanthosoma*. There appeared to be fusion of the innermost layer of cells near the stigma in taxa in *Chlorospatha* sect. *Chlorospatha*, and along the attenuated portion below the stigma in species in *Chlorospatha* sect. *Occidentales*.

The mantle is somewhat deliquescent after female anthesis, with the surface becoming visibly liquid and the free portions of broadly spreading mantles collapsing against the ovary walls. However, the substance and form persist to some extent, through the pollen cycle and even after abscission of the spathe blade and fertile male portion of the spadix. Some vestiges of the mantle were visible in the early fruiting stages in some cases. Understanding of the overall function of the mantle, if a single function exists, remains elusive. It seems likely, considering the remarkable diversity of form and coloration observed that it serves more than one purpose or perhaps different purposes in different taxa. However, all would certainly relate directly to pollination biology. The diversity of coloration in the mantle and the fact that color reaches maximum intensity at

anthesis and is quite bright in numerous taxa, suggest that color serves an important purpose, perhaps as an attractant for pollinators. Madison (1978, 1981) suggested that the mantle possibly served as an osmophore, a notion that can probably now be discounted (see Spadix above), or to bridge the gap between pistils and thereby provide an even surface over which stigmatic fluid could flow freely from one flower to the next. The latter possibility could be the case in some but not most *Chlorospatha*. The margin of the mantle is usually not at all coherent with those of adjacent mantles in taxa in *Chlorospatha* sect. *Chlorospatha* nor in 12 species in section *Occidentales*, although a few mantles can be weakly coherent on spadices of some taxa in both sections. By “weakly coherent” we mean that some, but not all, margins of some adjacent mantles are contiguous. Most of the remaining species in *Chlorospatha* sect. *Occidentales* have mantles that are weakly coherent, leaving only 11 species in the genus with more or less consistently coherent mantles. Therefore, the notion that the mantles serve the purpose of providing a continuous surface for the flow of stigmatic fluid between flowers does not pertain in most *Chlorospatha*.

The density of arrangement of mantles is not correlated with the density of arrangement of ovaries, which can be laxly or densely arranged, regardless of the arrangement of the associated mantles, depending on the taxon. This is dramatically illustrated in *Chlorospatha castula* (*Chlorospatha* sect. *Occidentales*) in which the ovaries are markedly laxly arranged and the mantles 3 times wider than the ovary apex, with the margins coherent with those of adjacent mantles and, therefore, densely arranged. In *C. kolbii* (*Chlorospatha* sect. *Chlorospatha*), the ovaries are laxly arranged and the mantle is narrow, with the margins not at all coherent. The density of arrangement of pistils, in our descriptions, refers only to arrangement of the ovaries, with that of the styles noted separately.

The style is not expanded into a mantle in species in Category B, which includes all species in *Chlorospatha* sect. *Orientales* and can be further divided into two groups. In one group comprised of *C. cutucuensis*, *C. portillae*, and *C. sizemoreae*, the style is briefly attenuated and as broad as or moderately narrower at the base than the ovary apex, with the margin obscure (Style Type 2, Fig. 1). Attenuation is not as pronounced as in most styles in *Chlorospatha* sect. *Occidentales*. Red chromoplasts were a primary means of distinguishing the stylar region from the ovary in pickled material of *C. cutucuensis*, although Madison (1981) describes the style as yellowish in living material. No chromoplasts were observed in the

dried or pickled material of *C. portillae* or *C. sizemoreae*. In the second group (Style Type 1, Fig. 1) comprised of *C. boosii*, *C. engleri*, *C. hannoniae*, *C. limonensis*, *C. longipoda*, *C. plowmanii*, *C. pubescens*, and *C. yaupiensis*, the styles are not usually attenuated, but obscure attenuation was observed in living material of *C. engleri* and some collections of *C. longipoda*, and possibly occurs in other species in this group. Styles in this group are as broad as or weakly narrower than the ovary apex, extremely thin, though somewhat thicker and tougher than the ovary walls, with the margins weakly or not at all coherent with those of adjacent styles.

The style and its margin are frequently difficult to distinguish from the ovary. Even in living material, the margin is difficult to discern in *Chlorospatha plowmanii* and *C. sizemoreae*, in which coloration of the style and ovary is identical and the typical rimlike margin is apparently obscure or absent. However, the margin is usually easily discernible in dried material in all species. Coloration and a surface texture that is different from that of the ovary serve to easily distinguish the style in living material of *C. boosii*, *C. engleri*, *C. hannoniae*, and most collections of *C. longipoda* and *C. pubescens* in the second group, and in *C. cutucuensis* and *C. portillae* in the first group. In these species, the surface is usually somewhat colliculate (comprised of minute subhemispherical elevations) and appears somewhat matte or even velvety in living material, and less glossy than the ovary. In *C. plowmanii*, *C. sizemoreae*, and some collections of *C. longipoda* and *C. pubescens*, this texture was lacking. Red chromoplasts are usually visible in both living and dried styles in the second group of species and are helpful in determining the stylar region. The style of *C. limonensis* is known only from pickled material and that of *C. yaupiensis*, only from dried material. The styles in this group (Category B) are possibly homologous to the discoid styles found in *Xanthosoma*. In both, the style lacks a mantle and is approximately as wide as the ovary apex; however, it is extremely thin and weakly or not at all coherent with adjacent styles in *Chlorospatha* sect. *Orientales*, but is thick and coherent in *Xanthosoma*.

The stigma is sessile or apparently so in 30 taxa (Style Types 1, 3, and 4, Fig. 1), and more or less elevated on an attenuated style in 35 species (Style Type 2; Style Types 5–10). In taxa with sessile stigmas, living or pickled material must be examined microscopically (30×) to determine if the sessile condition is actual or merely apparent. The stigma was examined in living material of 23 species and pickled material of two additional species, and in all

cases were found to accord with Madison's (1978) description of the stigma of *Chlorospatha castula* as "brushlike." The stigma is densely papillate in *Chlorospatha*, as in most Araceae (Engler, 1920), with the papillae exceedingly thin and much longer than wide. In all living specimens examined, the individual papillae were clearly visible. In those species with elevated stigmas, the stigma was usually capitate or subcapitate, or cylindrical to obconical and truncate at the apex, or more or less coronate and broadly depressed medially, or in a few cases, weakly lobed. The shape of the stigma appeared to be disklike in dried material of a few species with elevated stigmas and in living material of *C. besseae*. More or less obconical stigmas that are broadest and truncate at the apex are also usually coronate and typical in *Chlorospatha* sect. *Orientales*. Stigmas in *Chlorospatha* sect. *Chlorospatha* are usually disklike and conspicuously wider than long, occupying half or occasionally more than half of the apical surface of the pistil. In *C. croatica* subsp. *croatica*, the disklike stigma was conspicuously coronate. In most *Chlorospatha*, the stigma is approximately as long as wide and usually between 0.2 and 0.7 mm in diameter, though some species with larger pistils can have stigmas almost 1 mm in diameter. Taxa in *Chlorospatha* sect. *Chlorospatha* frequently have stigmas 1 mm in diameter or slightly less.

Styles, including the mantle (when present), and stigmas, in both living and dried material, appeared undisturbed, with no signs of having been eaten by insects, in either wild or cultivated material. The living pistillate portions of the spadix in some species from all three sections were tasted and chewed at anthesis (by the second author) and lacked sweetness, pleasant or unpleasant flavor, or stinging quality. The living specimens sampled were few and no conclusions could be drawn. The stigma and all or some portion of the style persist in fruit.

Coloration. Coloration of the pistils is known in 32 species and is taxonomically significant, usually being a consistent character on the species level. In all cases, coloration is attributable to the style and is exceedingly diverse in *Chlorospatha*, with greatest diversity occurring in species in *Chlorospatha* sect. *Occidentales*, which also have the most varied and highly modified styles, with coloration confined to the mantle. In these species, the mantle can be white, cream, more or less green, bright orange, pinkish orange, rose-colored, purplish, yellow to yellowish, or pink. Coloration is somewhat less diverse in *Chlorospatha* sect. *Chlorospatha* in which the mantle can be white, cream-colored, or green, with two exceptions: *C. mirabilis*, with pink, yellow, or orange

mantles, and *C. callejasii*, with red mantles. In *Chlorospatha* sect. *Orientales*, a mantle is lacking and the style is white, cream, yellow, pale or medium green, or yellow-green in seven species, and white and densely dark purple-speckled in *C. hannoniae*. The color noted is always the perceived color, this being more significant in making determinations than actual color. As noted previously, the mantle, when present, can be exceedingly thin and, whether clear or to some degree colored, can therefore assume some of the coloration of the ovary or the main body of the style beneath it.

Coloration of the stigma is known in 21 species, 12 of which have white or cream-colored stigmas that can be somewhat greenish in three species. Exclusively greenish stigmas were observed in *Chlorospatha oblongifolia* and *C. sizemoreae*. The stigma of *C. bayae* is described as golden tan, but was possibly observed post-anthesis, similar coloration having been observed in numerous taxa after anthesis. Yellow or yellowish stigmas were observed in five species. Greatest variation was observed in *C. hastate*, with both orangish yellow and orangish white stigmas. In all cases, the stigma is somewhat translucent.

Style types. Style type is the most important gynoecial feature in *Chlorospatha* and frequently the critical delimiting character on the species level. The gynoecial classification presented in the present work is original and consists of 10 style types illustrated in Figure 1. Although the stigma is, with few exceptions, somewhat uniform superficially, the style is highly morphologically diverse. Each style type, except Type 7 (Fig. 1), is represented by at least one species, frequently more, known from living or pickled material, and although most taxa are known only from dried material, the drying characteristics of presumably similar taxa known from living or pickled material have been applied to interpretations of these. In most cases, the morphology of dried styles corresponds to that of living styles and only in rare instances, when pistils were poorly preserved, are style types deduced from what were considered other relevant factors, such as associated floral structures and/or their arrangement. Style type was determined in all taxa except Species 1–4, *C. munchiquensis*, and *C. queremalensis*, with only fruiting material available of *C. munchiquensis* and neither fruiting nor fertile material available of the remaining species.

FRUITS AND SEEDS

In the 27 species of *Chlorospatha* in which an infructescence was present, the developing pistils

were contained within the closed spathe tube after anthesis and pollination, presumably until fully ripe, with the tube persisting and ultimately separating at the margins at maturity. Mature infructescences with ripe berries were observed in only approximately half of these species, but these represent all sections and, therefore, all known floral morphologies in the genus. The spathe tube enlarges to accommodate the developing berries that eventually force the margins of the tube apart, thereby exposing the ripe berries (see Spathes, above).

The berries of *Chlorospatha* are depressed-globose, as long as wide or somewhat wider than long, and more or less 2- to 4-furrowed (or 5-furrowed [Mayo et al., 1997]), with the furrows usually coinciding with the position of the locule walls and their number equal to the number of locules. Remnants of the stigma are persistent, and the margins of the style are clearly visible on ripe berries, also occasionally some remnants of the mantle as the berries develop, in those taxa with a mantle. The size of the berries is known in 21 species and is between 1.5 and 5 mm long, and 2 and 5 mm in diameter, in most cases. The berries of *C. dodsonii* are as much as 7 mm in diameter, the largest in the genus, possibly to accommodate the numerous seeds that usually occur in this species, which, although usually 3- to 4-locular, can have as many as 15 ovules per locule, the greatest number observed in locules of plurilocular ovaries in *Chlorospatha*. Berries are fleshy in *Chlorospatha*, with the seeds usually clearly visible through the sides, which are quite thin and easily ruptured.

Nothing is known about fruit dispersal in *Chlorospatha*. Dehiscence is apical and the mesocarp surrounding the seeds is gelatinous and sticky, which would suggest animal or bird dispersal. It is not known if flavor or fragrance occurs in the ripe berries. Coloration of the berries is known in only 10 species, but could possibly provide some clues regarding dispersal. The berries are entirely greenish white, pale green, or creamy green in four species, *C. atropurpurea*, *C. engleri*, *C. gentryi*, and *C. stellaris*, but can also be yellow in *C. atropurpurea*. Greenish yellow berries were reported for *C. narinoensis*. The cream or pale green berries of *C. longipoda* (Croat et al. 86561) were violet-tinged and those of *C. plowmanii* (Croat et al. 88008A) purple-speckled. In *C. croatian* subsp. *croatiana*, *C. cutucuensis*, and *C. dodsonii*, the berries were white. The absence of orange or red berries in this sample is possibly significant.

Little is known about the seeds of *Chlorospatha*. However, those observed were minute, ovoid to

ellipsoid and terete, or slightly obtusely 3-sided (Croat et al. 86561), white to somewhat creamy in color or pale green (Croat et al. 88008A), somewhat brownish when dry, and contained copious amounts of endosperm (Mayo et al., 1997). Seeds were 1–2 mm long and 0.8–1 mm in diameter, with the testa longitudinally costate except in *Croat et al. 88008A*, a collection of *C. plowmanii* from the eastern slopes of the Andes in Ecuador, in which the testa was smooth. Smooth seeds are possibly typical of this species, but the seeds of this collection were the only ones of this species available for examination. Grayum (1986) noted that seeds of *C. croatian* were brown-strophiolate and that there were 15 to 25 in each berry. Most ovaries of this species are 3-locular, with seven to 10 ovules per locule, the number of ovules corresponding well with the number of seeds observed. Such is not the case in *C. cutucuensis* and *C. longipoda*, wherein the number of seeds is significantly less than the number of ovules. In *C. cutucuensis*, the ovaries are 3- to 4-locular, with four to 10 ovules in each locule, yet only three to five seeds (mostly three) were observed in the berries (Madison, 1981). There are seven to eight seeds in berries of *C. longipoda* in which most ovaries are 2- to 3-locular, with eight to 12 ovules per locule. Madison (1981) suggested, regarding *C. cutucuensis*, that this disparity in the number of ovules and seeds might indicate recent evolution toward an increase in seed size and a decrease in the number of seeds. However, it is possible that not all ovules were properly pollinated, and when berries are carefully examined, the remains of undeveloped ovules are frequently observed. It is possibly significant that these dissimilar species, *C. cutucuensis* and *C. longipoda*, are from the eastern slopes of the Andes in Ecuador, whereas *C. croatian* is from Central America. The largest seeds were observed in *C. longipoda*, these being as much as but frequently less than 2 mm long. However, this is not significantly larger than the maximum length of 1.5 mm observed in other taxa.

The embryo is elongate and axile in *Chlorospatha* (Mayo et al., 1997).

POLLINATION BIOLOGY

Little is known about the pollination biology of *Chlorospatha* in the wild, beyond reports that flies and small beetles (Scarabaeidae, Staphylinidae) have been collected in the inflorescences (Madison, 1981). Mayo et al. (1997) list only Staphylinidae as possible pollinators. Label notes for *L. Bittner 2493* (MO) indicate that black beetles pollinate *C. bogneri*; however, it is possible that the beetles were merely

present in the spathe and are not necessarily the true pollinators. Staphylinidae are often found in rotting fruit but more frequently in rotting animal and vegetable matter in which they lay their eggs, and the adults and their larvae feed on flies and fly larvae, possibly on other beetle larvae (Dr. Bob Woodruff, pers. comm.). Interestingly, Julius Boos (pers. comm.), an expert on beetle behavior, suggests that the Staphylinidae are possibly attracted either by the usually fruity fragrance of the *Chlorospatha* inflorescence or by the flies that are attracted to that fragrance, and thereby become coincidental pollinators as they feed on the flies. It would seem equally plausible that the flies themselves are the pollinators and that the presence of the Staphylinidae is entirely coincidental. However, pollen is essentially smooth, not spinose, in *Chlorospatha*, and smooth pollen is generally correlated with pollination by beetles, whereas spinose pollen is correlated with pollination by flies (Grayum, 1984, 1985, 1990). None of the sterile flowers or parts of the pistils had been eaten in the living or dried material examined by the authors, which frequently occurs in association with pollination by beetles. Grayum (1990) noted that protogyny is frequently seen in association with beetle pollination. As with most Araceae, the flowers are strongly protogynous in *Chlorospatha*, with the stigma receptive approximately 12 to 24 hours before the onset of anther dehiscence, with the phases not overlapping. In cultivation, pollen was frequently observed in the spathe tubes during and after anther dehiscence.

Prior to this treatment, it was generally assumed that at anthesis, the spathe of *Chlorospatha* opened only narrowly on the blade portion, which would greatly limit the size of pollinators, the spathe tube typically being quite narrow (pre-anthesis), usually less than 1 cm in diameter. During a period of one to seven years, the authors studied 19 diverse species representing the full geographical distribution and presumably most if not all pollination strategies in the genus, and observed conditions contrary to those described by Madison (1981) (see Spathes, above). The entire spathe opened either narrowly to broadly at anthesis, with the opening comprising between two thirds and three fourths of its length in seven species, to within 1–2 mm of the base in seven species, and in all cases, had some or most of the pistillate portion of the spadix exposed. In five species, only the blade opened more or less broadly at anthesis, with some of the apical portion of the tube also open (Fig. 6B), usually exposing some of the pistillate portion of the spadix, to as much as one third of that portion in some species. Even when the pistillate portion is not visible from a forward position, it is clearly visible

when viewing from above since the apex of the tube is much expanded at anthesis. Although the considered sample is small, exposure of some of the pistillate portion at anthesis is apparently significant, this being the predominant condition in the sampled taxa. It is possible that exposure of the pistils is coincidental to the increased accessibility to pollinators afforded by the openness and considerable increase in size of the spathe tube.

Coloration of the pistils is diverse, attributable to the style, frequently intense and often considerably different from that of the fertile and sterile male portions of the spadix (see Spadix above). Color is most intense at anthesis and clearly visible in most taxa observed. For color to be manifest implies, to some level of certainty, that it is necessary. While it might be possible for colors to be differentiated at night, it would require spectral perception beyond the norm, on the part of pollinators, specifically perception of infrared, ultraviolet, or both wavelengths. There are no studies of color perception in beetles, but ultraviolet perception is possibly involved, many flowers in various families having clearly marked ultraviolet pathways invisible to the human eye, leading to the sexual areas of the flowers (Dr. Bob Woodruff, pers. comm.). It is more likely that color in *Chlorospatha* flowers evolved to appeal to conventional visual perception. Since color-differentiating sight cells, compared to broad-spectrum (black-and-white) light-sensing cells, are traditionally inversely sensitive to light by a factor of 100,000 to one, it is generally accepted that animals with good color vision are primarily diurnal or active in high light times. Considerable visual acuity is sacrificed for color perception; therefore, it seems likely that color plays a critical role in what must certainly be a diurnal pollination syndrome in *Chlorospatha*, all known relevant factors indicating such a syndrome.

The spathe began to open after dawn, between 0600 and 1000 hours of day 1, and was fully expanded by 1200 to 1400 hours in the 18 species examined. The expansion and disposition of the spathe as it approaches and reaches anthesis were observed in the wild and confirmed in most species examined and in a number of additional species that were not observed over time or in cultivation. This behavior coincides with the onset and subsequent increase in intensity of fragrance observed in 17 of the 18 species (see Sterile Flowers above). No fragrance was detected in *Chlorospatha plowmanii*, although the species has the same pattern of spathe expansion. Both conditions were affected by the amount of available light, and on overcast days, the onset and development of both were somewhat

delayed; therefore, the discrepancies in timing noted above are possibly correlated with available light or other prevailing conditions rather than with species-specific behavior. Fragrance peaked between 1200 and 1400 hours and was noticeably diminishing by approximately 1700 hours and undetectable by nightfall of day 1. It is possible that fragrance persists, but is not detectable by human beings, and, in fact, faint fragrance was detected on day 2 and day 3 of the flowering event in two species, *C. hannoniae* and *C. kolbii*, which was possibly attributable to pollen or the decay of floral structures.

The following is a detailed though somewhat imprecise analysis of the flowering strategies observed in nine species representative of the three sections of *Chlorospatha*. Each section has a distinct floral morphology; however, the various flowering strategies do not appear to be exclusive on the sectional level, even within this small sampling, except possibly in *Chlorospatha* sect. *Orientales*. Observations of inflorescences were made over a period of three to four days, at 1- to 2-hr. intervals beginning at 0400 hours and terminating at approximately midnight. In *C. mirabilis*, the flowering of only four inflorescences in a single sympodium was observed (Croat & Mora 83686).

In *Chlorospatha kolbii*, a member of *Chlorospatha* sect. *Chlorospatha*, the spathe opened on day 1, as described above, and remained open to the same degree, through the first night and until approximately 1700 hours on day 2, with the diameter of the apex of the spathe tube maintained at approximately twice the diameter of the spadix (Fig. 28B). At 1700 hours on day 2, the spathe was beginning to close slightly and pollen was being produced, with the apex of the tube sufficiently open to allow a clear view of the pistils until approximately midnight. At 0600 hours on day 3, the spathe had completely though somewhat loosely closed. The flowering strategy described above is identical to that observed in *C. atropurpurea*, a member of *Chlorospatha* sect. *Occidentales*, but with the diameter of the apex of the spathe tube 3 to 4 times greater than that of the spadix at 1800 hours on day 1.

In *Chlorospatha dodsonii*, another member of *Chlorospatha* sect. *Occidentales*, the flowering strategy was the same as that described above on day 1, but with a slight occlusion of the spathe tube at 2000 hours, leaving only the apex open. At 0600 hours on day 2, some pollen was visible and the tube had closed slightly, but the pistils were clearly visible from its apex. The spathe remained in this slightly closed position through the night of day 2, and at 0600 hours on day 3 the fertile staminate portion of

the spadix was covered with pollen. At noon, the pollen had collapsed, but no further constriction of the apex of the tube was observed. At 0600 hours of day 4, the spathe was closed. In *C. mansellii* (Fig. 35C), possibly a primary hybrid with *C. dodsonii* as one of its parents, the strategy was similar except for a somewhat greater occlusion of the tube at 1800 hours on day 1 and during day 2, and in the timing of anther dehiscence, which did not begin until 1400 hours on day 2 and continued until 2000 hours on day 3. At 0600 hours on day 4, the pollen had collapsed and the spathe was loosely closed.

Four species in *Chlorospatha* sect. *Orientales* were observed, *C. hannoniae*, *C. longipoda*, *C. plowmanii*, and *C. pubescens*, all exhibiting the same basic flowering strategy, one different from those described above. It is noteworthy that the spathes of these species are among the smallest in the genus and open almost to the base at anthesis on day 1. The process on day 1 was the same as that described above until 1800 to 2200 hours. At this time, the sides of the spathe tube were closed, occluding the pistillate portion of the spadix, but the apex of the tube was slightly open, with a diameter approximately 2 mm greater (ca. 2 times wider) than that of the spadix and the pistils visible (looking down the tube). The disposition of the spathe was the same throughout the night of day 1 and most of day 2, with some pollen visible at 1800 hours on day 2. At 2000 hours on day 2, pollen covered the fertile staminate portion of the spadix, and the diameter of the apex of the tube was approximately 1 mm greater than that of the spadix. At noon on day 3, the spathe was closed and the pollen had collapsed. *Chlorospatha plowmanii* differed from the other species in several respects, most notably in the post-anthesis disposition of the spathe blade, which was starting to reflex by 2000 hours on day 1 (Fig. 41D), frequently earlier, and by 0400 hours of day 2, was completely reflexed (Fig. 41B). Anther dehiscence began at approximately 1200 hours on day 2 in *C. plowmanii*, six hours earlier than in the other three species, and continued for 42 hours on some occasions, until 0600 hours on day 4. The spathe blades of the other species in *Chlorospatha* sect. *Orientales* remained more or less erect to erect-spreading, but with that of *C. pubescens* occasionally assuming a spreading position, but persisting in that position until abscission of the fertile staminate portion of the spadix, the typical condition in *Chlorospatha*. In *C. plowmanii*, the blade was quickly deciduous, abscising soon after anthesis, frequently before it had completely withered.

The flowering strategy of *Chlorospatha mirabilis*, a member of *Chlorospatha* sect. *Chlorospatha*, was

similar to that of the four species in *Chlorospatha* sect. *Orientales* on day 1 of the flowering event, with the apex of the tube approximately 2 times wider than the spadix at anthesis and with a diameter only 2 mm wider than that of the spadix at 2100 hours. At 2300 hours on day 1, the only portion of the spathe that remained open was a narrowly elliptical one on the blade portion. At 0600 hours on day 2, the apical halves of the spathe and spadix were prominently curved forward and almost U-shaped. Anther dehiscence began at approximately 0700 hours on day 2, with the opening in the blade 2 cm long and 5 mm wide, and at 1030 hours the fertile male portion of the spadix was covered with pollen and the blade was loosely closed. Pollen had collapsed at 1600 hours on day 2.

The pollination strategies described are not precise and could not presently be considered distinct or representative of all possible strategies in *Chlorospatha*. There is considerable variation in the timing and amount of spathe expansion and occlusion in any given species, even in single plants, on different occasions. However, in the absence of any information regarding these conditions, the limited information provided here should prove useful in future investigations. In all strategies, female anthesis occurred during the day on day 1, with little or no occlusion of the spathe tube in *C. kolbii* and *C. atropurpurea*, slight occlusion in *C. dodsonii*, and moderate occlusion in *C. mansellii* until the end of day 2 of the flowering event. The openness of the tube through female anthesis and anther dehiscence is indicative of the marked protogyny of the flowers, no self-pollination having been observed in the four species cited above, during three to seven years in cultivation, though pollen falls onto the pistils during each flowering cycle.

In *Chlorospatha mirabilis* and the four species in *Chlorospatha* sect. *Orientales*, the spathe tube was significantly more occluded than in the other species at 1800 to 2200 hours on day 1 (post-anthesis), but with the apex slightly open and remaining so through anther dehiscence. In spite of the narrower apex of the spathe tube after female anthesis, pollen was observed within the tube during and after anther dehiscence. Greatest constriction of the tube occurred near the base of the sterile portion of the spadix in these five species. This possibly serves as a well for dislodged pollen that accumulates, through which pollinators could presumably pass as they exited the tube. No such accumulation or mechanisms for accumulation were observed in *C. atropurpurea* or *C. kolbii*. In *C. dodsonii* and *C. mansellii*, the condition is intermediate between that observed in *C.*

atropurpurea and *C. kolbii* and that observed in the species in *Chlorospatha* sect. *Orientales*, with the tube apex less occluded than in the last two species and more occluded than in *C. atropurpurea* and *C. kolbii*. In *C. dodsonii* and *C. mansellii*, the greatest constriction occurred along the length corresponding to the entire length of the sterile portion of the spadix, and in the latter species, the constriction was sufficient to allow pollen accumulation at 0600 hours on day 3. In all cases, when the spathe closes, it is less turgid than at or prior to anthesis and easily manipulated, though somewhat less so on the tube than on the blade, which suggests that any pollinators that might remain could easily escape. The tube is more rigid throughout the process in *C. mansellii* and species in *Chlorospatha* sect. *Orientales*.

The timing of the processes in the flowering event is similar in most species examined, with the onset of anther dehiscence in the late afternoon to early evening on day 2, approximately 24 hours after termination of female anthesis, and continuing for 12 to 18 hours, with the pollen collapsing by noon on day 3. *Chlorospatha dodsonii*, *C. mansellii*, *C. mirabilis*, and *C. plowmanii* are exceptions. Pollen production began approximately 12 hours after female anthesis and continued for approximately 34 hours in *C. dodsonii*, until afternoon on day 3. Anther dehiscence began approximately 20 hours after female anthesis and continued for approximately 32 hours in *C. mansellii*, until after midnight on the morning of day 4. In *C. mirabilis*, anther dehiscence began 12 hours after female anthesis and continued for approximately 10 hours. In *C. plowmanii*, anther dehiscence began 18 hours after female anthesis and continued for approximately 42 hours, until early morning on day 4.

The flowering event, from the onset of anthesis until the pollen collapses and the spathe closes, requires 34 to 48 hours or slightly more, to as much as 54 to 72 hours, depending on the species. The patterns described in each strategy are somewhat artificial and not entirely distinct from each other, particularly as regards the onset and duration of anther dehiscence, which begins approximately 12 to 24 hours after termination of female anthesis and continues for approximately 10 to 42 hours, depending on the species. However, the duration of female anthesis appears to be consistent in all species examined and, as treated herein, is circumscribed by the onset of spathe expansion and emission of fragrance and some subsequent occlusion of the spathe and termination of fragrance emission, a period of approximately 12 hours. At the end of this period, the stigma and style deliquesce and are

presumably no longer receptive. However, the receptive period is possibly considerably less than 12 hours long, since full spathe expansion and maximum fragrance emission are brief, lasting no more than a few hours. The stigma and pollen are somewhat sticky, as is the style, though only weakly so, in all species examined except those in *Chlorospatha* sect. *Orientales*, which lack a mantle. No resin canals were observed in the spathe. Minute fluid droplets, slightly more viscous than water and faintly acrid in taste, were observed on the inner surface of the spathe tube from the beginning of day 2 through the end of anther dehiscence, which possibly assists in the adherence of pollen to the bodies of beetles. No fluid droplets were observed during day 1, but the inner surface of the tube was almost imperceptibly tacky. However, the droplets are possibly attributable to condensation caused by thermogenesis in the spadix within the confines of the spathe tube. The presence or absence of thermogenesis, the rapid oxidation of stored starch or lipids (Walker et al., 1983; Gottsberger, 1990), could not be confirmed. Thermogenesis or other attractants associated with the staminate spadix presumably exist during anther dehiscence, possibly both, to ensure pollen collection and dispersal, particularly in *C. atropurpurea* and *C. kolbii*, wherein the apex of the spathe tube is open broadly for two days and pollinators could conceivably come and go at will. Considering the apparent absence of mechanisms for entrapment and the length of time between termination of anthesis and onset of anther dehiscence in these two species, and to some extent in *C. dodsonii* and *C. mansellii*, it is possible that some form of reward is provided in these and other species, which causes the pollinators to remain in the spathe tube through the pollen cycle. Clearly, a significant amount of fieldwork is needed in this area of study, during which the behavior of the pollinators would, no doubt, answer most of the many questions raised.

PHENOLOGY

No field-oriented studies of phenology have been conducted for *Chlorospatha*, and the pollination biology of most species is poorly known; therefore, no broad base of information exists from which a comprehensive understanding of the relevant processes involved in flowering might be deduced. Twenty-seven species are known only from single flowering collections and five additional species from sterile collections or those with only infructescences or no collection dates reported. In taxa represented by two or more collections, flowering was usually

staggered, with one to many months between recorded flowerings, or occasionally occurred in consecutive months, rarely in the same month. To imply any seasonality in flowering based on so few collections would be misleading and, at this time, any apparent patterns are best attributed to the timing of collections. Based on the historical record of herbarium collections, the greatest number of taxa flowered during the period from July through August, with 23 and 17 flowering taxa recorded, respectively, for those months. Twenty-one taxa flowered in April, 18 in November, and 17 in December. The least number of flowerings is recorded for January, with fertile collections of only seven species. For each of the remaining months, between 11 and 15 flowering taxa were recorded.

It is possibly significant that the seven species represented by numerous collections from habitat flowered in almost every month and possibly flower throughout the year: *Chlorospatha atropurpurea*, *C. croatianana* subsp. *croatiana*, *C. dodsonii*, *C. ilensis*, *C. longipoda*, *C. plowmanii*, and *C. pubescens*. Although only five flowering months were recorded for *C. mirabilis*, it is possible that this species also flowers throughout the year. That flowering can occur in almost every month would seem to accord with the more or less constant climatic conditions in the consistently mesic habitats occupied by *Chlorospatha*. Twelve species, including seven of the eight mentioned above, excluding *C. mirabilis*, were observed in cultivation in a state of presumably legitimate flowering cycles considered sufficiently healthy and robust that could be verified and recorded. The records made during cultivation of these seven species correspond to the historical record of flowering of these species in the wild. Flowering is virtually continuous in some cultivated species in *Chlorospatha* sect. *Orientales*, with flowering occasionally occurring on almost every new growth in *C. plowmanii*. Another cultivated species, *C. kolbii*, flowered during seven months, but could not be maintained in a sufficiently healthy state to confirm flowering (or not) throughout the year. Plants were cultivated at approximately 28°N latitude and maintained at 15.5°C–30°C (60°F–86°F) throughout the year. *Chlorospatha* occurs at approximately 10°20'N–4°16'S latitude, where the photoperiod is considerably less variable than at the higher latitude of the cultivated plants, but other as yet undetermined conditions are undoubtedly more variable than those provided in cultivation. Variation in the amount of precipitation would presumably be an important factor, as would the availability of pollinators, which possibly coincides with variations

in precipitation. Dry seasons occur in some areas that support populations of *Chlorospatha*, but these are neither prolonged nor what could be considered “dry.” Precipitation is either somewhat reduced overall or occurs less frequently and thus provides some variation in prevailing conditions, however slight.

Three cultivated species consistently exhibited periodic flowering cycles every year during a four- to seven-year period. *Chlorospatha mansellii* flowered only during the months of October and November. *Chlorospatha boosii* and *C. hannoniae* flowered only between May and September. In all three species, flowering was vigorous, coinciding with almost every new leaf growth. In *C. mansellii*, only two to three new leaves are produced during its flowering season, whereas in the two small-growing species, more numerous leaves were produced, production and maturation of leaf growth being more rapid in the these species, which raises an interesting point. As has been stated previously, growth is more or less continuous throughout the year in *Chlorospatha*, but the rate at which new leaves are produced and mature varies among taxa and is presumably, to some extent, correlated with the mature size of a given taxon. Large-growing species produce fewer leaves during the year and each leaf requires more time to mature than the smaller and more numerous leaves of small-growing species. Therefore, it is likely that some taxa flower throughout the year, but that individual plants are not necessarily in flower in every month, particularly as regards large-growing species, which is almost certainly the case in *C. croatiana* subsp. *croatiana*. The periodic flowering of the three aforementioned species cannot be explained, but similar cycles probably occur in the wild in other, poorly known species. *Chlorospatha boosii* and *C. hannoniae* are sympatric with *C. longipoda*, probably also with *C. plowmanii* and *C. pubescens*, yet flowering is virtually continuous in the last three species, both in the wild and in cultivation. *Chlorospatha boosii* and *C. hannoniae* were collected in a sterile state, in the month of March, a month in which these species would also have been sterile in cultivation.

Fruiting phenology in *Chlorospatha* is too poorly known to report on here. Fruit presumably develops fairly rapidly in the small inflorescences of species in *Chlorospatha* sect. *Orientalis*, which reach anthesis in quick succession. In these species, developing infructescences were observed in sympodia with inflorescences, with apparently ripe infructescences in the sympodium immediately below (Figs. 4B, 19D). In this case, maturation could conceivably

occur in a matter of weeks, vegetative growth in these relatively small-growing species being quite rapid. It is assumed that more time would be required for the maturation of larger infructescences.

CYTOLOGY

No karyological studies were made for this revision. Keating (2003) reported $2n = 26$ for the three species he studied, which corresponds to the finding of Bogner (1985) for *Chlorospatha corrugata*. Mayo et al. (1997) also report $2n = 26$.

GEOGRAPHICAL DISTRIBUTION AND ENDEMISM

Chlorospatha occurs from Costa Rica and Panama in Central America, southward through northwestern South America into southern Ecuador and would be expected to occur in the Amazonian regions of Peru and Colombia, possibly also in southeastern Nicaragua in Central America.

Greatest diversity is found at elevations of 1000–2000 m in Colombia and southward to the western Andes of northern Ecuador, with progressively fewer species encountered to the south on the western slope, but with considerable diversity on the eastern slopes of the Andes in Ecuador. Diversity diminishes also in northernmost Colombia into Central America. Colombia has 45 taxa, Ecuador 24, Panama three, and Costa Rica one. Endemism is highest in the Cordilleras Occidental and Central in Antioquia and Valle departments of Colombia, with 34 endemic species, almost all of which are associated with the Cordillera Occidental. Ecuador has 23 endemic species, 11 occurring only on the western slopes of the Andes and 12 only on the eastern slopes. Central America has two endemic species, one of which is endemic to Panama.

Greatest diversity in *Chlorospatha* occurs in Colombia with 45 taxa (66% of all taxa), 43 of which are endemic (93%). Twenty-four species, 23 of which are endemic (96%), occur in Ecuador, a remarkable number for an area one fourth the size of Colombia. The relatively high number of Ecuadorian species is somewhat misleading and probably reflects more extensive collecting over a longer period of time, with 226 total collections made and most species represented by numerous collections. Many Colombian species are represented by only one or two collections. Future collecting, comparable to that done in Ecuador, would be expected to result in many new collections, including new species, considering the vastness of the geographical area and the presence of a profound diversity of geological and ecological elements that could support *Chlorospatha*,

and thus provide a better understanding of distribution and endemism in that country.

Chlorospatha occurs between sea level and 3000 m elevation, with most taxa occurring only in the wet to very wet areas of tropical wet forest (Holdridge, 1967), premontane wet forest, lower montane wet forest, tropical rainforest, premontane rainforest, lower montane rainforest, or montane rainforest, with few taxa reported from the somewhat drier areas of tropical moist forest, premontane moist forest, and lower montane moist forest. The taxa that occasionally occur in these drier life zones are mainly confined to the eastern slopes or the southern portions of the western slopes of the Andes in Ecuador, the current southern limit of distribution in the genus. Sixty percent of all taxa occur exclusively or occasionally in premontane wet forest, the predominant life zone for the genus, approximately 30% in tropical wet forest, and 30% in tropical rainforest, premontane rainforest, or montane rainforest.

Diversity diminishes southward in Ecuador, on the increasingly drier Pacific slopes of the Andes. Most of the area along the coast, south of the equator, is tropical dry forest (T-df), tropical very dry forest (T-vdf), or even tropical thorn woodland (T-tw) and would not support *Chlorospatha*. *Chlorospatha* has been collected in most provinces on the western slopes, excluding Loja on the southwestern border; however, only three species have been collected in the provinces that lie south of Pichincha Province, *C. atropurpurea*, *C. dodsonii*, and *C. ilensis*, relatively widespread species that also occur northward, at least into Pichincha Province in Ecuador. The life zones indicated by the GPS coordinates of some collections of these species, made in the southern or coastal provinces, are clearly not conducive to *Chlorospatha* and are presumably erroneous. It has been the experience of the authors that small pockets of suitable habitat frequently occur within broader, incompatible hostile regions. In fact, some suspect coordinates fall quite near suitable areas. The coordinates for some collections of *C. ilensis* fall in montane dry forest (TM-df) or premontane dry forest (P-df) in El Oro Province, and tropical dry forest in Los Ríos, whereas the coordinates of most collections of this species indicate premontane wet forest, occasionally premontane moist forest or lower montane moist forest. Even these last two life zones are unusual for *Chlorospatha* and are, with few exceptions, confined to collections of some species from the eastern slopes of the Andes, made within the pervasive moist forest ecology in that portion of the Amazon drainage. A similar diminution of diversity to

the south does not occur on the eastern slopes where more or less mesic conditions prevail. Diversity is actually somewhat more limited in the northern provinces of Napo and Sucumbíos in Ecuador, with three and five species, respectively, and is greatest to the south, with nine species in Morona-Santiago Province. Collections have been made in all provinces on the eastern slopes in Ecuador, many near and along the length of the Peruvian border, and *Chlorospatha* will undoubtedly be found in Peru, since there are few geological or ecological barriers to distribution there.

Only three taxa (two species, one variety) are recorded for Panama and one species for Costa Rica (*Chlorospatha croatiana* subsp. *croatiana*), and these occur in tropical wet forest, premontane wet forest, lower montane wet forest, and montane wet forest, also premontane rainforest and lower montane rainforest or transitional forest between these. Of these (*C. croatiana* subsp. *croatiana*, *C. croatiana* var. *enneaphylla*, *C. hammeliana*, and *C. mirabilis*), only *C. croatiana* subsp. *croatiana* and *C. hammeliana* are endemic to Central America, but the first species will probably eventually be collected in South America, possibly also in southeastern Nicaragua. Central America has been well collected, 55 collections of *Chlorospatha* having been made there. *Chlorospatha* occurs throughout Panama, with the exceptions of Herrera and Los Santos, which are generally too dry, comprised primarily of areas that are drier parts of tropical moist forest as well as tropical dry forest and premontane moist forest, all life zones in which *Chlorospatha* does not occur in Central America. The three taxa are members of *Chlorospatha* sect. *Chlorospatha* and, therefore, share similar floral and vegetative morphology. The similarities of these taxa, the absence of dissimilar species, and the pronounced dry seasons in the areas west of Costa Rica and southeastern Nicaragua would suggest that southern Central America is the northern limit of the genus and that *Chlorospatha* probably originated and evolved in Colombia.

Far greater diversity occurs in Colombia, possibly reflecting its isolation from Central America during periods when the oceans were at much higher levels than today and it was not connected to Central America, with subsequent development occurring from Colombia into Panama after the emergence of the isthmus. Similarly, since no species of *Chlorospatha* occurs on both the eastern and western sides of the Andes, the evolution of the respective Amazonian and Pacific taxa presumably occurred independently, after the Andes began to rise toward the end of the Cretaceous (Raven & Axelrod, 1974).

As treated herein, taxa of the western slopes of the Andes include those occurring in the Magdalena River drainage; therefore, *C. huilensis* could be considered the exception to the exclusivity of eastern and western Andean taxa, its collection sites being uniquely situated at the southern end of the Cordillera Oriental, where it joins the Cordilleras Central and Occidental in the Andean range and the separation of the Cordilleras Central and Oriental is no longer distinct. All but one of the collections of this species were made on what could be loosely considered either the western slopes of the Cordillera Oriental or eastern slopes of the Cordillera Central, within the Magdalena River drainage, in montane rainforest and lower montane rainforest, with access to further distribution onto the eastern slopes of the Andes within a broad band of lower montane wet forest with broad extensions of montane rainforest around the perimeter. One collection was made in lower montane wet forest to the south, between Pasto and Mocoa, in the Amazon drainage and represents the northernmost collection of *Chlorospatha* on the eastern slopes of the Andes. The species bears a strong resemblance to *C. sucumbensis* from Sucumbíos Province, Ecuador, collected in lower montane wet forest near the Colombian border on the eastern slopes of the Andes. Styler morphology in both species is distinct from that of all Amazonian species, which suggests that these probably originated in the Magdalena River drainage and not the eastern slopes of the Andes. As such, *C. huilensis* and *C. sucumbensis*, the only members of *Chlorospatha* sect. *Occidentales* that occur in the Amazon drainage, represent the only existing link between the eastern and western taxa. Only from this point southward, in Ecuador, does *Chlorospatha* develop on the eastern slopes, though apparently not from these two species or their progenitors. The remaining species from the eastern slopes comprise *Chlorospatha* sect. *Orientales* and manifest several distinctive characters not found in other *Chlorospatha*. These species are clearly members of *Chlorospatha*, possessing numerous characters unique to the genus, but apparently evolved independently of the taxa that developed in the Colombian mountain ranges. It is likely that some species in *Chlorospatha* sect. *Orientales* occur at the latitudes of *C. huilensis* in southern Amazonian Colombia, possibly northward in lower montane wet forest or premontane wet forest, the predominant life zones on the eastern slopes of the Cordillera Oriental, north of the areas where *C. huilensis* was collected.

It is curious that only *Chlorospatha huilensis* and one other taxon are reported from the Cordillera Oriental in Colombia, *C. croatiana* var. *enneaphylla*,

which is the only taxon from Boyacá Department and occurs only once on the western slopes of the Cordillera Oriental, approximately 370 km north of the collections of *C. huilensis*, with no collections of *Chlorospatha* having been recorded for the extensive intervening area. The area south of this collection site, to the approximate latitude of Bogotá, is mostly lower montane dry forest with intervening patches of montane moist forest and lower montane moist forest that could possibly contain *Chlorospatha*. The area from Bogotá southward to the Ecuadorian border is apparently not conducive to populations of *Chlorospatha* and the void there would appear to reflect collecting patterns. Although most of the basin of the southern Magdalena River drainage is tropical dry forest and the lower western slopes of the Cordillera Oriental are regions of premontane moist forest, the areas above these are tropical wet forest, lower montane wet forest, montane wet forest, and montane moist forest. The area north of Tunja, on the western slopes in Boyacá Department, north of the collection site of *C. croatiana* var. *enneaphylla*, is comprised of large areas of premontane moist forest and premontane wet forest, with montane wet forest in Santander Department, north of Boyacá Department, all of which could possibly support *Chlorospatha*, but the areas have apparently been poorly collected in Colombia.

The current isolation of the Central and South American taxa is more problematic, since the forest elements and consistently wet conditions required by *Chlorospatha* are present in southern Central America, and no prominent geological barriers exist between the two areas. The northwestern part of Chocó Department in Colombia that borders Panama consists of several floristic elements. Most of the vast drainage area of the Río Atrato, which empties into the Golfo de Urabá in the north, lies only a few meters above sea level and consists of tropical moist forest near the coast that transitions into tropical wet forest toward the south and eventually tropical rainforest farther south, near Quibdó. Annual precipitation often exceeds 11,700 mm in the region of tropical rainforest (Gentry, 1982). The Serranía de los Saltos and Serranía Baudó serve as the western perimeter of the Río Atrato drainage for much of its length, extending from the Panamanian border southward, along the Pacific Coast in Colombia. These are not high mountain ranges and only the Alto de Buey reaches approximately 1000 m elevation. The Cordillera Occidental represents the eastern perimeter of this lowland region. The entire region, including the coastal ranges, is heavily forested, but the tropical rainforest does not extend to the Pacific

coast and is displaced by a narrow band of tropical wet forest along the coast. It would appear that low elevation and the somewhat drier conditions north of the region of tropical rainforest were possibly significant limiting factors, with this region serving as a barrier to distribution of the more numerous species of the Colombian mountain ranges. Of the 12 Colombian taxa that occur only below 1000 m elevation (26% of Colombian taxa), nine occur in the lowlands of Chocó Department, including *C. croatian* var. *enneaphylla* and *C. mirabilis*, the only taxa common to both Central and South America, and of these, six species are endemic in this department. The remaining three species occur in lowland areas in Valle and Cauca departments immediately south of Chocó.

Sixty percent of all *Chlorospatha* (41 species) occur only above 1000 m elevation and almost half of these also occur above 2000 m, with 13% of all taxa occurring only above 2000–3000 m (Croat, pers. obs.). Within Colombia, greatest taxonomic/species diversity occurs in the region from the northern ends of the Cordilleras Occidental and Central in Antioquia Department, southward to Cali in Valle Department, with 34 taxa represented, almost half of all *Chlorospatha*. Of these, 60% occur only above 1000 m elevation in the Cordilleras Occidental and Central and apparently have not diversified into the vast lowland forests between the Cordillera Occidental and the mountains in Panama or the Serranías de los Saltos and Baudó along the Pacific Coast of Colombia. Only three species, *C. croatian* var. *enneaphylla*, *C. corrugata*, and *C. mirabilis*, have been collected below 1000 m elevation in the area from the Panamanian border southward, between the Pacific coast and the Cordillera Occidental, to the approximate latitude of Quibdó, more than 200 km south of the Panamanian border. The first taxon occurs near sea level, near Acandí, at the northern end of the region, near the Panamanian border in Colombia, in transitional forest between premontane wet forest and tropical moist forest. The other two species, *C. corrugata* and *C. mirabilis*, occur in the Nutibara area in Antioquia Department, in premontane rainforest at 890–900 m elevation on the western slopes of the Cordillera Occidental. Interestingly, *C. corrugata* is the only Colombian endemic that occurs both below and above 1000 m elevation (890–1350 m) and could not be considered a lowland species. The collection of *C. mirabilis* is somewhat suspect, being morphologically atypical of the species and the only collection of this species made on the eastern side of the lowland region, and therefore, possibly another species. The three taxa, *C. croatian* var.

enneaphylla, *C. corrugata*, and *C. mirabilis*, are confined to the perimeter of the region in question. It is only at and below the latitude of Quibdó, approximately 5°45'N, that the other lowland taxa (from below 1000 m) occur, as well as the remaining populations of *C. mirabilis*, and are more widely dispersed through the lowlands: *C. chocoensis*, *C. grayumii*, *C. hastifolia*, *C. kolbii*, *C. kressii*, *C. maculata*, *C. morae*, *C. oblongifolia*, *C. timbiquensis*, *C. yatacuensis*, and *Chlorospatha* sp. indet. 2. Possibly of significance is the fact that the tropical rainforest more or less begins at this point, near the latitude of Quibdó, and extends southward, coinciding with a reversal of the river drainage system. An almost imperceptible ridge located near Istmina, south of Quibdó, is responsible for this reversal from the north-flowing Río Atrato drainage to the south-flowing Río San Juan drainage that empties into the Pacific. The northernmost western collection of *C. mirabilis* was made at the southern end of the Serranía Baudó, near the latitude of Quibdó, where all modern collections of *C. kolbii* were also made, and it is possible that this low coastal range provided the conditions necessary for distribution into Central America. Certainly, these species would be expected to occur northward in the range. At present, it appears that *Chlorospatha* evolved in the montane regions of Colombia and developed into distinct floras on the eastern and western sides, with the rising of the Andes (Croat, pers. obs.). The western ancestral forms subsequently diversified into the tropical rainforest, but not the tropical wet forest or tropical moist forest to the north, in the western lowlands of Chocó Department, with the low coastal Pacific range ultimately serving as a bridge for distribution into Panama. Admittedly, the lowland region from Quibdó northward has not been well collected, and except for the collections made by A. Forero and A. Gentry in the late 1970s and early 1980s, few botanists have visited the area; therefore, the notion that the region serves as a barrier to distribution is possibly derived from a coincidental absence of pertinent information.

Chlorospatha croatian var. *enneaphylla* occurs in Panama and in Colombia on the eastern border with Panama, with distribution eastward into the northern end of the Cordillera Central and to the south, on the western slopes of the Cordillera Oriental, and it seems plausible that it evolved in Panama. However, the possibility of evolution in and distribution from the east should be considered, perhaps with evolution of the taxon occurring independently of the species. Diversity of taxa with divided leaf blades is concentrated in the region of the Cordilleras Occidental and Central in Antioquia Department,

and it would seem that distribution could have occurred from either or both sides of these mountain ranges, given the necessary ecological conditions. The floral morphology common to all taxa, i.e., the small slender inflorescences often with long peduncles and tightly enveloped by the petiole sheath with divided leaf blades (except *C. corrugata*), reinforces this possibility. The three Colombian populations of *C. croatiana* var. *enneaphylla* are widely separated geographically and occur in an unusually wide range of life zones, though all are below 900 m elevation, with the collection from the Cordillera Oriental made in premontane wet forest and those from the Cordillera Central in what is either premontane rainforest or tropical wet forest. The northern population on the Panamanian border is in transitional forest between premontane wet forest and tropical moist forest. It is possible that these apparently disjunct populations approached contiguity in earlier times, when the life zones were possibly less disparate, or that later encroachment of unfavorable ecological or human elements caused subsequent isolation of the populations. It is also possible that intervening areas have not been collected.

Seventeen taxa of *Chlorospatha* (24%) occur only below 1000 m elevation and are herein described as lowland taxa (Croat, pers. obs.). Interestingly, of the 12 lowland taxa in Colombia, seven have divided leaf blades (*C. chocoensis*, *C. croatiana* var. *enneaphylla*, *C. kolbii*, *C. kressii*, *C. maculata*, *C. mirabilis*, *C. morae*), and although there are no truly wide-ranging *Chlorospatha*, two of these, *C. mirabilis* and *C. croatiana* var. *enneaphylla*, are significantly more wide-ranging than most *Chlorospatha*, occurring widely within Colombia and extending into Panama, though at higher elevations in Panama. Excluding the Panamanian taxa, the remaining group of nine species of *Chlorospatha* with divided blades, with one exception (*C. ilensis*), are confined to elevations of 1200–2800 m in the Cordilleras Occidental and Central and occur only in Antioquia Department, with five endemic species (*C. betancurii*, *C. callejasii*, *C. cogolloi*, *C. gentryi*, *C. luteynii*), and the two departments on its southern border: Caldas, with one endemic species (*C. caldasensis*), and Risaralda, with two endemic species (*C. cedralensis* and *C. risaraldensis*). No species with divided blades occurs to the south of these departments except *C. ilensis*, the northernmost collection of which was made over 500 km to the south, on the western slopes of the Andes in Pichincha Province, Ecuador. Although some collections of *C. ilensis* have hastate or subhastate leaf blades, other collections have 3-lobed blades, thus rendering it the only 3-lobed species in Ecuador.

This species shares the distinct floral morphology of all taxa in *Chlorospatha* sect. *Chlorospatha* (i.e., blades trifid, trisect, pedatifid, or pedatisect; sessile stigmas with Style Type 3 where the style is expanded into a more or less disklike mantle approximately as broad as the ovary apex). The isolation of this Ecuadorian endemic cannot be explained; however, it is one of the more wide-ranging species in Ecuador, in terms of geography and elevation, occurring in Pichincha and four provinces to the south, at 550–1530 m elevation.

A similar pattern of wide distribution is found in six of the additional seven Ecuadorian species that occur both below and above 1000 m elevation, *Chlorospatha atropurpurea*, *C. dodsonii*, and *C. litensis*, from the western slopes of the Andes, and *C. longipoda*, *C. plowmanii*, and *C. pubescens* from the eastern slopes. Of these, *C. litensis* is the only species not endemic to Ecuador, occurring also in southern Colombia, only above 1000 m elevation, but only below 1000 m in Ecuador. Interestingly, there is little or none of the variation in the floral or vegetative morphology that would be expected in these species throughout their considerably diverse elevational ranges and life zones. The three species from the eastern slopes occur between 250 and 1700 m elevation, usually in tropical wet forest, premontane wet forest, and lower montane wet forest, occasionally in premontane rainforest, and rarely in tropical moist forest, premontane moist forest, and/or montane moist forest. *Chlorospatha hastata* occurs at 375–1800 m elevation, but is known only from Esmeraldas and Carchi provinces and, therefore, does not fit the pattern of wide distribution described above. All of the aforementioned Ecuadorian species and the lowland Colombian taxa are apparently more adaptable in the wild than most *Chlorospatha*, considering the diversity of elevations and life zones in which they occur, and most have proven relatively easy to maintain in cultivation. The five Ecuadorian species that occur only below 1000 m elevation, *C. besseae*, *C. longiloba*, and *C. mansellii* from the western slopes, and *C. boosii* and *C. hannoniae* from the eastern slopes, also adapt well to cultivation, but would appear to be rather narrowly distributed, each being known from only one or two provinces, which is somewhat puzzling, particularly as regards the Amazonian species, since species of Amazonian Araceae are usually more wide-ranging, especially those from the large areas of tropical moist forest in the Amazon Basin (Croat, 1998). The narrow distribution of the two Amazonian species possibly reflects both undercollecting and life zone ecology. *Chlorospatha boosii* is the only species from the

eastern slopes that has been collected in the pervasive tropical moist forest of that region, though most species occur at least once in premontane moist forest, which is true of *C. hannoniae*, as well as in numerous wetter life zones. However, Ecuador has been well collected compared to Colombia, and life zone ecology is probably a significant factor in the high level of provincial endemism exhibited in these and other Ecuadorian species and presumably the even greater levels of departmental endemism indicated in the Colombian species, particularly regarding those species confined to elevations exceeding 1000 m. *Chlorospatha* can be found in small, isolated pockets of suitable forest, as was the case with *C. sagittata*, which was encountered unexpectedly on the western slopes in Imbabura Province, in a small patch of forest associated with a small stream by a road bordered by large remnants of partially disturbed virgin forest. It is endemic to and the single species known from that province.

Chlorospatha sagittata was collected at almost 1700 m elevation and is one of 11 species in Ecuador that occur only above 1000 m elevation (between 1200 and 2350 m), each of which is endemic to a single province: *C. carchiensis*, *C. castula*, and *C. jaramilloi*, also from the western slopes, and *C. cutucuensis*, *C. engleri*, *C. feuersteiniae* (Croat & Bogner) Bogner & L. P. Hannon, *C. limonensis*, *C. sizemoreae*, *C. sucumbensis*, and *C. yaupiensis* from the eastern slopes. Of these, only two species occur above 2000 m elevation, *C. jaramilloi*, in premontane wet forest, and *C. sucumbensis*, known only from above 2000 m in montane or lower montane wet forest. Coordinates (GPS) indicate that *C. sizemoreae* possibly also occurs occasionally or exclusively above 2000 m elevation, but no elevation was indicated in the label notes for this species. These species are known from only one or two collections and might eventually prove to be more widely distributed, except perhaps *C. cutucuensis* and *C. yaupiensis*, which are known only from the lower montane wet forest of the Cordillera de Cutucú, an area known for a high level of endemism in Araceae. This mountain range lies in Morona-Santiago Province in which nine of the 11 species in *Chlorospatha* sect. *Orientales* occur, including *C. cutucuensis* and *C. yaupiensis*, which suggests that these species evolved in this region. The two remaining species in the section, *C. portillae* and *C. sizemoreae*, are known only from Zamora-Chinchipe Province immediately to the south, in the vicinity of El Panguí, in premontane wet forest and lower montane wet forest, respectively. Greatest diversity in Ecuador occurs in Morona-Santiago, with nine species, six of which are endemic:

C. boosii, *C. cutucuensis*, *C. engleri*, *C. hannoniae*, *C. limonensis*, and *C. yaupiensis*.

Forested areas that can support *Chlorospatha*, which have been isolated by human encroachment, are frequently encountered throughout Colombia and Ecuador and could explain actual or apparent endemism in some cases. Additionally, it appears that almost all South American collections have been made around cities, along roads or in national parks, which is well illustrated in the region of the Cordillera Occidental, from approximately 4°N latitude in Colombia southward to the Ecuadorian border. *Chlorospatha* has not been recorded from the western slopes of the Cordillera Central or the valley of the Río Cauca to the east at these latitudes, these areas being quite arid in general. At the aforementioned latitudes, all collections were confined to the eastern or western slopes of the Cordillera Occidental, in three widely separated areas directly or closely associated with one of only three existing major roads in the Cordillera Occidental, with no collections recorded for the intervening areas. Greatest diversity occurs at the northern end of this region, around Calí in Valle Department and westward along the road to Buenaventura on the coast, with 10 of the 12 species occurring there being endemic to the department. Nine of these species occur only above 1000 m elevation (1020–2200 m) usually in tropical wet forest, premontane wet forest, or lower montane wet forest, or occasionally in tropical rainforest or premontane rainforest. The endemic species are: *C. bayae*, *C. bullata*, *C. caliensis*, *C. noramurphyae*, *C. queremalensis*, *C. stellasarrae*, *C. tokioensis*, *C. yatacuensis*, *Chlorospatha* Species 2, and *Chlorospatha* Species 3. The southernmost collection of *C. mirabilis* was made in this area.

The area around Parque Nacional Munchique lies to the south, in Cauca Department in Colombia, along a road running westward from the Pan-American Highway, and represents the greater portion of a second area of diversity. Four species are endemic to the department, *Chlorospatha congensis*, *C. lehmannii*, *C. munchiquensis*, and *C. timbiquensis*, and one species occurs also in Chocó and possibly Valle, *C. grayumii*, in tropical wet forest and tropical rainforest. *Chlorospatha munchiquensis* occurs within the park, in premontane wet forest and lower montane wet forest, whereas *C. congensis* and *C. lehmannii* occur outside the park, probably in premontane rainforest.

An isolated region to the south, in Nariño Department, represents the third area of diversity in Colombia, with seven species, six of which are

endemic: *Chlorospatha bogneri*, *C. nambiensis*, *C. narinoensis*, *C. planadensis*, *C. ricaurtensis*, and Species 1. *Chlorospatha litensis* also occurs here in premontane wet forest and in northernmost Ecuador in premontane wet forest and lower montane rain-forest. All collections were made along or near the road that runs from the Pan-American Highway westward to the coast, near and almost parallel to the border with Ecuador, at between 1100 and 2050 m elevation. Most collections were made in either the La Planada Reserve, in lower montane wet forest or premontane wet forest, or Río Ñambí Reserve, in premontane wet forest. In Ecuador, excluding Morona-Santiago Province, which has the greatest number of species (nine), the greatest concentration of species, as to province, occurs in the two provinces adjoining this area on the western slopes, Carchi and Esmeraldas. Of the 12 species known from the western slopes in Ecuador, six occur only in one or both of these provinces, *C. besseae*, *C. carchiensis*, *C. hastata*, *C. litensis*, *C. longiloba*, and *C. mansellii*, or in the case of *C. litensis*, also in Nariño Department, Colombia. A total of seven species occur in Esmeraldas and six in Carchi. Species that occur only in the provinces of Ecuador and departments of Colombia that lie along the length of their common border have been designated herein as frontier species, and all would be expected to occur in the adjoining country. No geographical barriers are present and the varied ecological conditions that occur at any point along the border are similar or identical on both sides. A separate key to these species has been provided (see Key to Species of *Chlorospatha*, below). Pichincha Province, to the south of the frontier region, and Zamora-Chinchipe, on the eastern slopes of the Andes in the southeast, hold the next highest concentrations of species in Ecuador, with five species occurring in each province. Two species are endemic to Pichincha and one species to Zamora-Chinchipe. Between one and four species are reported for each of the remaining provinces, none of which is endemic, except as previously noted.

Sixty-four percent of all *Chlorospatha* are found exclusively on the western slopes of the Cordillera Occidental in Colombia and the Andes in Ecuador. In Colombia, most taxa are confined to the Cordillera Occidental: with 72% of Colombian taxa (33 species) occurring only on the western slopes; one species, *C. giraldoi*, occurring on both the eastern and western slopes; and two species occurring only on the eastern slopes, *C. macphersonii* and *C. noramurphyae*. *Chlorospatha corrugata* is the only species that occurs on the western slopes of both the Cordillera

Occidental and Cordillera Central. Seven species occur only in the Cordillera Central: two known only from the eastern slopes, *C. amalfiensis* and *C. betancurii*; two known only from the western slopes, *C. caldasensis* and *C. cedralensis*; two known only from the northern end, *C. callejasii* and *C. luteynii*; and one known from both the eastern and western slopes, *C. antioquiensis*. *Chlorospatha croatian* var. *enneaphylla* also occurs here, but is also known from Panama, northern Chocó Department, and the western slopes of the Cordillera Oriental. The greatest concentrations of taxa occur in Antioquia and Valle departments, Colombia, each with 12 taxa, with 10 endemic in each department; followed by Chocó with 10 taxa, six of which are endemic; Nariño with seven species, six of which are endemic; and Cauca with six species, four of which are endemic. These statistics coincide with the high number of total collections made in these departments, which is significantly greater than the number made in other departments. The greatest number of collections was made in Antioquia with 40 collections, followed by Chocó with 28 collections, Valle with 27 collections, Nariño with 24 collections, and Cauca with seven collections (Croat, pers. obs.). It is possible that the high number of taxa in Antioquia and Valle departments is coincidental to the greater number of collections made there. However, considering the diversity of the floral and vegetative morphology of the taxa involved, it seems more likely that the perceived significance of the numbers, regarding evolution of the genus, is actual rather than coincidental and affirms the opinion (of the authors) that *Chlorospatha* originated in and evolved from these regions in the Cordilleras Occidental and Central. Development in Nariño Department appears to be aligned with that of the northwestern Ecuadorian species, with the combined area serving as a subsequent secondary center of development.

Two species occur in Risaralda Department in Colombia, both of which are endemic. One species occurs in each of the remaining departments, Boyacá, Caldas, Huila, and Putumayo, none of which is endemic to a department except *Chlorospatha caldasensis*, from Caldas Department. *Chlorospatha* is not known from the departments east of the Cordillera Oriental, except Putumayo, nor from those north of Antioquia, though *Chlorospatha* possibly occurs into Córdoba, at the northern limit of the Cordillera Occidental, along the border with Antioquia. No taxa have been reported from the five departments in and between the Cordilleras Central and Oriental: Cundinamarca, Norte de Santander, Quindío, Santander, and Tolima, but *Chlorospatha*

Table 1. *Chlorospatha* species and section distributions in Costa Rica (CR), Colombia (COL), Ecuador (ECU), and Panama (PAN).

Species	Section	Country
<i>amalfiensis</i>	<i>Occidentales</i>	COL
<i>antioquiensis</i>	<i>Occidentales</i>	COL
<i>atropurpurea</i>	<i>Occidentales</i>	ECU
<i>bayae</i>	<i>Occidentales</i>	COL
<i>besseae</i>	<i>Occidentales</i>	ECU
<i>betancurii</i>	<i>Chlorospatha</i>	COL
<i>bogneri</i>	<i>Occidentales</i>	COL
<i>boosii</i>	<i>Orientales</i>	ECU
<i>bullata</i>	<i>Occidentales</i>	COL
<i>caldasensis</i>	<i>Chlorospatha</i>	COL
<i>caliensis</i>	<i>Occidentales</i>	COL
<i>callejasii</i>	<i>Chlorospatha</i>	COL
<i>carchiensis</i>	<i>Occidentales</i>	ECU
<i>castula</i>	<i>Occidentales</i>	ECU
<i>cedralensis</i>	<i>Chlorospatha</i>	COL
<i>chocoensis</i>	<i>Chlorospatha</i>	COL
<i>cogolloi</i>	<i>Chlorospatha</i>	COL
<i>congensis</i>	<i>Occidentales</i>	COL
<i>corrugata</i>	<i>Occidentales</i>	COL
<i>croatiana</i>	<i>Occidentales</i>	COL, CR, PAN
<i>croatiana</i> ssp. <i>croatiana</i>	<i>Chlorospatha</i>	CR, PAN
<i>croatiana</i> var. <i>enneaphylla</i>	<i>Chlorospatha</i>	COL, CR, PAN
<i>cutucuensis</i>	<i>Orientales</i>	ECU
<i>dodsonii</i>	<i>Occidentales</i>	ECU
<i>engleri</i>	<i>Orientales</i>	ECU
<i>feuersteiniae</i>	<i>Occidentales</i>	ECU
<i>gentryi</i>	<i>Chlorospatha</i>	COL
<i>giraldoi</i>	<i>Occidentales</i>	COL
<i>grayumii</i>	<i>Occidentales</i>	COL
<i>hammeliana</i>	<i>Chlorospatha</i>	PAN
<i>hannoniae</i>	<i>Orientales</i>	ECU
<i>hastata</i>	<i>Occidentales</i>	ECU
<i>hastifolia</i>	<i>Occidentales</i>	COL
<i>huilensis</i>	<i>Occidentales</i>	COL
<i>ilensis</i>	<i>Chlorospatha</i>	ECU
<i>jaramilloi</i>	<i>Occidentales</i>	ECU
<i>kolbii</i>	<i>Chlorospatha</i>	COL
<i>kressii</i>	<i>Chlorospatha</i>	COL
<i>lehmannii</i>	<i>Occidentales</i>	COL
<i>limonensis</i>	<i>Orientales</i>	ECU
<i>litensis</i>	<i>Occidentales</i>	COL, ECU
<i>longiloba</i>	<i>Occidentales</i>	COL
<i>longipoda</i>	<i>Orientales</i>	ECU
<i>luteynii</i>	<i>Chlorospatha</i>	COL
<i>macphersonii</i>	<i>Occidentales</i>	COL
<i>maculata</i>	<i>Chlorospatha</i>	COL
<i>mansellii</i>	<i>Occidentales</i>	ECU
<i>mirabilis</i>	<i>Chlorospatha</i>	COL, PAN
<i>morae</i>	<i>Chlorospatha</i>	COL
<i>munchiquensis</i>	<i>Occidentales</i>	COL
<i>nambiensis</i>	<i>Occidentales</i>	COL
<i>narinoensis</i>	<i>Occidentales</i>	COL
<i>nicolsonii</i>	<i>Occidentales</i>	COL
<i>noramurphyae</i>	<i>Occidentales</i>	COL
<i>oblongifolia</i>	<i>Occidentales</i>	COL
<i>planadensis</i>	<i>Occidentales</i>	COL

Table 1. Continued.

Species	Section	Country
<i>plowmanii</i>	<i>Orientales</i>	ECU
<i>portillae</i>	<i>Orientales</i>	ECU
<i>pubescens</i>	<i>Orientales</i>	ECU
<i>queremalensis</i>	<i>Occidentales</i>	COL
<i>ricaurtensis</i>	<i>Occidentales</i>	COL
<i>risaraldensis</i>	<i>Chlorospatha</i>	COL
<i>sagittata</i>	<i>Occidentales</i>	ECU
<i>sizemoreae</i>	<i>Orientales</i>	ECU
<i>stellasareae</i>	<i>Occidentales</i>	COL
<i>sucumbensis</i>	<i>Occidentales</i>	ECU
<i>timbiquensis</i>	<i>Occidentales</i>	COL
<i>tokioensis</i>	<i>Occidentales</i>	COL
<i>yatacuensis</i>	<i>Occidentales</i>	COL
<i>yaupiensis</i>	<i>Orientales</i>	ECU
Indets.		
sp. indet. 1	<i>Occidentales</i>	COL
sp. indet. 2	<i>Occidentales</i>	COL
sp. indet. 3	<i>Occidentales</i>	COL
sp. indet. 4	<i>Occidentales</i>	COL

would be expected to occur in at least some of these, particularly in the montane wet forest in Santander Department.

Collection of additional taxa in Central America would not be expected. Although Ecuador has seen more extensive collecting over a longer period of time than Colombia, the recent experience (of the authors) indicates that many suitable areas have not been investigated and that discovery of additional species is likely. The ultimate number of species of *Chlorospatha* can only be surmised, when or if the vast, less easily accessible, and unexplored montane areas are reached, particularly those in Colombia. The Amazonian areas, both montane and lowland, of Peru and Colombia will surely eventually prove to contain members of the genus, possibly some new to science. See Table 1 for species and sectional distribution.

TAXONOMIC TREATMENT

I. *Chlorospatha* Engl., Gartenflora 27: 97. 1878, tab. 933. TYPE: *Chlorospatha kolbii* Engl.

Caladiopsis Engl., Bot. Jahrb. Syst. 37: 140. 1905. TYPE: *Caladiopsis lehmannii* Engl.

Terrestrial, evergreen herb, occasionally \pm arborescent and 0.3–2 m tall or hemiepiphytic and 0.3–4 m, occasionally emergent aquatic, occasionally in small colonies, rarely widespread; growth sympodial, polyphyllous; new growth sylleptic, the first leaf a sylleptic prophyll; stem unbranched, fleshy, caulescent, elongate, erect or decumbent and

epigaeous, usually in part subterranean, with cataphylls retained intact, semi-intact or \pm fibrous along part or all of its length or only at upper nodes, or not at all, occasionally also or only with remnants of old petiole bases persisting \pm intact or fibrous; fibers \pm linear, pale to medium brown; sap milky or transparent, rarely pink; bulbils absent or produced randomly along its length, solitary, rarely in clusters of two to six, $5\text{--}20 \times 3\text{--}12$ mm, emerging green, becoming brown, cylindrical, conical or ovoid, \pm acute at apex or rounded and briefly attenuate; internodes \pm cylindrical, $0.5\text{--}8 \times 0.5\text{--}4$ cm, usually as long as or slightly longer than wide (1–2 cm long), occasionally much longer or shorter than wide, usually glabrous, occasionally scurfy, rarely weakly and minutely costate near nodes or with the epidermis peeling back, matte to glossy, pale to dark green, yellow-green, olive-green, brownish or grayish green, occasionally purple-tinged or brown, rarely red, occasionally becoming entirely brown with age or only at nodes; roots adventitious along the length of stem, usually white to greenish, occasionally pinkish green, the cortex comprised of unligified parenchyma cells lacking resin canals; cataphylls attached around circumference of stem, (1)2 to 4, produced with each new leaf or only with sympodial leaves, marcescent and persistent or quickly to ultimately deciduous, narrowly triangular to narrowly lanceolate, frequently weakly to prominently inequilateral, acute, acuminate or cuspidate at apex, or more frequently obtuse with acumen or apical or subapical apiculum, entirely obtusely or acutely 1- to 2-ribbed abaxially or in part only at or toward apex, thin but firm, occasionally \pm fleshy (in larger taxa), glabrous, rarely puberulent (*Chlorospatha pubescens*), matte to semiglossy, pale to medium green, rarely dark green, occasionally pink, purple, purple-tinged or purple- or dark green-mottled in narrow transverse bands. LEAVES with spiral phyllotaxy, several to numerous, long-petiolate, erect to erect-spreading, occasionally also spreading to reflexed-spreading (in some species); sympodial leaf a fully expanded foliage leaf or cataphyll; **petioles** lacking a geniculum, 10–125 cm, as long as or longer than blades, spongy to moderately firm, rarely brittle (*C. maculata*), usually glabrous, entirely or in part \pm puberulent or pubescent in some species, occasionally entirely minutely many-ribbed or in part only in the free portion, entirely green, purple or purplish brown, or green and purple-tinged or purple-, brown-, black-, or dark green-mottled in narrow transverse bands, rarely brown, gray-mottled, reddish pink or with a glaucous bloom toward the base,

sheathed basally, (1/10 to) 1/4 to 3/4 of or nearly entire length (1/3 to 2/3 in ca. 70% of taxa), usually less on juvenile and foliage leaves than on sympodial leaves; sheath decurrent or free-ending at apex, occasionally with one side decurrent and the opposite side free-ending; sides convolute or erect to erect-spreading with margins erect or in-rolled, rarely broadly spreading and appearing winged; free portion 3–10 mm diam. midway (usually less than 5 mm), entirely or in part terete, subterete or D- or U-shaped with margins acute and occasionally raised, or obtuse, rarely with acute lateral ribs becoming alate toward the apex (*C. kolbii*), entirely or in part sulcate or not, with or without a low medial keel; **blades** with supervolute vernation, 9.5–62 cm, entire and oblong, ovate or ovate-elliptic, rounded or acute at the base and occasionally inequilateral, or simple and cordate, sagittate, subsagittate, hastate or subhastate and weakly to prominently or not at all constricted in area of petiole attachment, or variously divided and trifid or pedatifid, auriculate or not, or compound and trisect or pedatisect, membranaceous to coriaceous, rarely fleshy (*C. macphersonii*), glabrous, weakly to conspicuously bicolorous, maculate in some species, the margins \pm smooth, occasionally weakly sinuate, occasionally broadly to narrowly undulate or crispate-undulate; upper surface smooth and flat, wrinkled or quilted, or corrugate, bullate, sub-bullate, or rugose, velvety to glossy, medium to markedly dark green, yellow-green, olive-green, or grayish green, rarely purplish medially or entirely brown, occasionally with dark purple-brown, punctiform or cream-colored, punctiform or pale linear cellular inclusions; lower surface \pm smooth, reticulate or rarely areolate, occasionally narrowly colliculate along all orders of venation, glossy to matte-subvelvety, \pm green, occasionally purple, purple-tinged, purple-mottled, or discolorous and dark purple along midrib and major veins; venation colocasioid, occasionally reticulate; midrib and major veins usually flat and featureless on upper surface, rarely bluntly angular or convex, moderately to deeply or narrowly sunken, occasionally obtusely sunken, rarely etched or etched-sunken, glabrous, rarely sparsely puberulent (*C. pubescens*), moderately to prominently raised on lower surface, variously shaped in cross-section, occasionally minutely many-ribbed or 1-ribbed medially, \pm green and concolorous or weakly to conspicuously paler or darker than surface, occasionally purple, purple-tinged or purple-mottled in narrow transverse bands; midrib concolorous on upper surface, occasionally paler than surface; primary lateral

veins pinnate, in 2 to 11 pairs, concolorous on upper surface, occasionally paler than surface, rarely weakly darker than surface (*C. sizemoreae*), conspicuous on lower surface, \pm straight, arcuate, or irregularly ascending, loop-connected into submarginal collective vein; submarginal veins 2 to 4, the innermost \pm straight or weakly to prominently scalloped, occasionally remote from margin; **basal veins** coalesced into weak or prominent posterior rib, in pairs or branching off and acroscopic or basisopic; posterior rib (when present) well-developed, naked along the sinus or not, occasionally with the laminar tissue narrowly confluent on the posterior side at the base and obscuring petiole apex; interprimary veins occasionally present (in some species); minor veins structurally indistinct and entirely or in part flat, weakly to moderately sunken, etched, etched-sunken, or narrowly or obtusely sunken, glabrous, usually concolorous on upper surface, rarely with secondary veins weakly darker than surface (*C. sizemoreae*), entirely glabrous or entirely or in part \pm puberulent, granular-puberulent, or granulose on lower surface, concolorous, weakly paler or weakly to moderately darker than surface; secondary veins weakly to prominently raised or in part prominulous on lower surface; tertiary veins \pm raised, prominulous or flat and visibly distinct on lower surface; reticulate veins \pm raised or prominulous, or flat and visibly distinct or obscure on lower surface. **INFLORESCENCES** terminal (appearing axillary), erect to erect-spreading, emitting sweet fragrance at anthesis, rarely odorless (*C. plowmanii*), 2 to 8(to 10) per sympodium, emerging successively at or near apex of petiole sheath or from a subtending sympodial cataphyll near the base; sympodial cataphylls marcescent, ultimately deciduous, 1- to 2-ribbed, glabrous, rarely puberulent (*C. pubescens*); peduncle usually longer than spathe, 10–88 cm \times 2–5 mm, usually 3 mm diam. or less, much shorter than to slightly longer than petiole, terete or occasionally variously shaped in cross-section, rarely in part sulcate, usually glabrous, rarely puberulent, subtended by inflorescence cataphyll; inflorescence cataphylls glabrous, whitish green, 1- to 2-ribbed abaxially; **spathe** surrounding spadix, occasionally curved somewhat forward, with margins convolute, weakly or not at all constricted between tube and blade, narrow, elongate, 3–20 cm, usually less than 1 cm diam., 10 to 20(to 25) times longer than wide, narrowly \pm cylindrical, ovoid or ellipsoid, frequently thicker than broad, longer than spadix, thin to thinly coriaceous, glabrous on inner surface, narrowly ovate, elliptical, or obovate when flattened

or with blade conspicuously narrower than tube, opening narrowly or broadly 2/3 to almost its entire length at anthesis or only \pm broadly on blade portion, narrowly to broadly funnel-shaped or tubular, remaining \pm open 1 to 3 days, frequently colorful, concolorous or weakly to prominently bicolorous on outer surface; spathe tube \pm cylindrical, ellipsoid or ovoid, occluding pistillate and most or all of sterile staminate portions of spadix, decurrent onto peduncle at base, as long as or occasionally shorter or longer than blade, persisting in fruit, glabrous on outer surface or \pm entirely or in part puberulent in some species, matte to glossy, white, cream, whitish, yellow, red, or purple, or \pm green and purple-tinged or not, matte to glossy on inner surface and concolorous or weakly to prominently paler than outer surface; spathe blade \pm erect or weakly to prominently cucullate, occasionally much longer than tube, frequently entirely obtusely 1-ribbed abaxially or in part toward apex (rib \pm acute toward apex), with margins \pm in-rolled (at anthesis), glabrous on outer surface, rarely in part puberulent, matte to glossy, white, cream, whitish, yellow, red, maroon, or purple, or \pm green and purple-tinged or not, matte to glossy on inner surface and concolorous or weakly to moderately paler, marcescent, rarely occasionally somewhat caducous (*C. plowmanii*), erect after anthesis, rarely spreading or reflexed, ultimately deciduous after anther dehiscence, rarely quickly deciduous after female anthesis (*C. plowmanii*); **spadix** monoecious, slender, 2.2–16.5 cm \times 2–8 mm, contained within and slightly to conspicuously shorter than spathe, \pm cylindrical or weakly thicker than broad, sessile or stipitate, \pm erect, frequently curved somewhat forward at anthesis, rarely also recurved midway and erect at apex (*C. congensis*), entirely or in part adnate to spathe at base, usually 1/2 or more of length of pistillate portion, occasionally also entirely or in part along length of sterile staminate portion, occasionally only along stipe, divided into pistillate portion at base and fertile male portion at apex, separated by sterile male portion, each portion with naked unisexual flowers arranged in spirals; stipe and axis usually \pm green, rarely dark violet, white or dark maroon; fertile male portion white, cream, yellow, bright orange, pink, red, green, dark purple, brown, yellowish, or greenish, the color frequently different from that of pistillate and sterile portions, cylindrical, tapering, ellipsoid, or clavate, 1.1–7.2 cm, as long as or shorter or longer than pistillate portion, usually much longer than sterile portion, densely flowered, occasionally with some flowers at apex

lacking microsporangia, rarely with 1 or 2 staminodes present (*C. atropurpurea*); sterile male portion white, cream, pink, green, yellow, yellow-orange, bright orange, dark purple, maroon, or purplish, (0–) 1–27 mm long or rarely lacking, weakly, moderately or conspicuously shorter than pistillate and fertile male portions, rarely longer (*C. atropurpurea*), occasionally weakly narrower than pistillate and fertile male portions, laxly or densely flowered; pistillate portion white, cream, yellow, green, orange, red, pink, maroon, rose-colored, yellowish, greenish, or purplish, with coloration attributable to the style and usually different from that of fertile and sterile male portions, \pm cylindrical or weakly broadest midway, 0.7–9 cm long, as long as or longer or shorter than fertile male portion, usually much longer than sterile male portion, rarely slightly shorter (*C. atropurpurea*), densely to laxly flowered, 1 to 6 flowers across axis (as viewed from above); stamens fused into synandria, with connectives thickened; thecae extending almost to the base, dehiscing by terminal pores or longitudinal slits; synandria densely arranged 1 to 2 (rarely less) \times 1–2.5(–3) mm, 2- to 6-androus (usually 3 or 4), deeply or shallowly lobed, obpyramidal, usually subprismatic and \pm regularly polygonal (viewed from above), \pm truncate at apex or occasionally broadly concave medially and moderately to prominently elongated in direction of axis, with margins of lobes thickened; pollen extruded in strands as permanent tetrahedral tetrads (rarely linear), inaperturate, starchless, binucleate, 33–48 μ m diam., psilate and obscurely punctate, obscurely verruculate, reticulate, foveolate-reticulate, smooth or variable-perforated, rarely with small holes; grains 24–29 μ m diam., spheroidal or subspheroidal; sterile flowers laxly or densely arranged, 0.5–2 \times 0.6–2.2 mm, comprised of free or fused staminodes lacking thecae, subprismatic, prismatic, evenly to irregularly lobed, branched or fungiform, with or without red chromoplasts; female flowers laxly or \pm densely arranged, (0.5–)1–3.2 mm; ovaries white, cream, green, or greenish, rarely dark maroon, lavender-tinged, or purple-streaked, usually \pm terete in cross-section, subglobose or obtusely conical, subcuboidal, ovoid, or obconical, 1.3–3.2 mm diam., usually narrowest at apex and as long as or weakly longer than wide, occasionally broadest at or near apex and as wide as long or ca. 2 times wider than long (in some species), (1)2- to 4-locular (possibly 5 or 6 in *C. mirabilis*), rarely plurilocular becoming unilocular toward the apex (*C. castula* and some *C. atropurpurea*); placentation axile, pseudoaxile or subaxile, rarely sub-basal or basal; ovules

anatropous or hemianatropous, presumably bitegmic, 0.15–0.22 mm, subhemispherical in longitudinal section or rarely dorsiventrally compressed and longer than wide, 3 to 14 in plurilocular ovaries, 8 to 20 in unilocular ovaries, 1- to 2(3)-seriate or disorganized, rarely 3- to 4-seriate (*C. lehmannii*), with funicles shorter, longer, or as long as ovules; styler region 0.3–2 mm, extremely short to conspicuously longer than ovary, as broad as or weakly to conspicuously broader than ovary apex, briefly to prominently attenuate and elongate, occupying 1/4 to 2/3 of the length of the pistil, or occasionally obscurely so or not at all, expanded or not into mantle, usually with red chromoplasts present; mantle (when present) frequently colorful, occluding and partially fused to main body of style, disklike, less than 0.5 mm long and as broad as to weakly broader or narrower than ovary apex, with margins usually not coherent with those of adjacent styles, or \pm attenuate or not, spreading, appressed to ovary or not, as broad as or weakly to conspicuously broader than ovary apex, with margins weakly to moderately coherent or not with those of adjacent styles, deliquescing after anthesis; **stigma** brushlike and densely papillate, white, cream, green, greenish, yellow, yellowish, golden tan, orangish yellow, or orangish white, 0.2–1 mm diam., usually about as broad as long, occasionally much broader than long (when disklike), sessile or apparently so, or weakly to prominently elevated on style, capitate, \pm cylindrical, obconical or disklike, occasionally weakly lobed, truncate or broadly depressed medially at apex, deliquescing after anthesis, persisting in fruit. **INFRUCTESCENCE** nutant, green, purple, or cream-colored, 4–12.5 \times 0.5–1.5 cm, 4 to 10(to 12) times longer than wide; berries exposed by re-opening spathe, depressed-globose, as long as wide or somewhat wider than long, 2- to 4(5)-furrowed, 1.5–5 \times 2–7 mm, fleshy, greenish white or cream, pale green, yellow-green, yellow or white, rarely violet-tinged green; seeds white, cream-colored or pale green, 3 to 25 per berry, 1–2 \times 0.8–1 mm, ovoid to ellipsoid, terete or obtusely 3-sided, longitudinally costate, rarely smooth; embryo axile, elongate; endosperm copious; chromosomes: $2n = 26$.

Chlorospatha consists of 69 taxa (68 species, one variety) from Costa Rica and Panama in Central America, and Colombia and Ecuador in South America. Ecologically, the genus is tropical, in perpetually wet areas in deep shade of forest understory, frequently along small streams, on steep banks or in boggy areas, at 0–3000 m elevation.

Etymology. From the Greek “chloro-,” meaning “green,” and “-spatha,” meaning “spathe,” referring to the spathe of the type *Chlorospatha kolbii*.

INFRAGENERA RELATIONSHIPS

Chlorospatha is not currently divided into sections or subgenera. However, the taxa fall into three natural and reasonably distinct groups, based on vegetative characters, floral morphology, and geographical distribution, with stylar morphology

serving as the primary delimiting character in these groups, based on the 10 distinct style types observed in the genus. The style type or types (see Style and Stigma Morphology) that occur in each group are exclusive to that group. Based on these findings, an original system of sectional classification is presented here, comprised of three sections: *Chlorospatha* sect. *Chlorospatha*, *Chlorospatha* sect. *Occidentales*, and *Chlorospatha* sect. *Orientales*.

KEY TO THE SECTIONS OF *CHLOROSPATA*

- 1a. Style expanded into a mantle; leaf blades erect to erect-spreading; ovaries longer than wide or as wide as long, not wider than long, usually plurilocular; rarely occurring on eastern slopes of the Andes.
 - 2a. Mantle disklike; stigma sessile or apparently so; ovaries usually longer than wide, plurilocular; leaf blades divided and simple or compound (with segments separated); not occurring on eastern slopes of the Andes *Chlorospatha* Engl. sect. *Chlorospatha*
 - 2b. Mantle spreading, not disklike; stigma usually elevated on style, rarely sessile or apparently so; ovaries as long as wide, plurilocular, rarely semi-unilocular; leaf blades entire or with posterior lobes, rarely trifid; rarely occurring on eastern slopes of the Andes *Chlorospatha* sect. *Occidentales* Croat & L. P. Hannon
- 1b. Style with mantle lacking; leaf blades erect to erect-spreading, or also spreading to reflexed-spreading (in some species); ovaries frequently wider than long, occasionally 1-locular; occurring only on eastern slopes of the Andes *Chlorospatha* sect. *Orientales* Croat & L. P. Hannon

1a. *Chlorospatha* Engl. sect. *Chlorospatha*, sect. nov. TYPE: *Chlorospatha kolbii* Engl.

Caudex plerumque erectus. Folia erecta vel erectopatentia; lamina trifida, trisecta, pedatifida vel pedatisecta, interdum maculata. Flos stylo in amiculum plus minusve disciforme latitudine ovarii apicem subaequans expanso; stigmatibus apparenter sessilibus.

Terrestrial or rarely hemiepiphytic, occasionally large and 1.5–2 m tall, not colonial; stem frequently erect. LEAVES (1)2 to 5, erect to erect-spreading; sympodial leaf a fully expanded foliage leaf; sides of petiole sheath convolute; blades trifid, trisect, pedatifid, or pedatisect, rarely with leaves not divided in some species (*Chlorospatha hammeliana*, *C. ilensis*), occasionally maculate. INFLORESCENCE with pistils \pm densely arranged, rarely laxly arranged; ovaries usually longer than wide, plurilocular; placentation axile, pseudoaxile, or subaxile (not basal); style expanded into disklike mantle, \pm truncate, rarely obscurely attenuate, occupying ca. 1/10 of the length of pistil (Style Type 3); margins conspicuous; stigma sessile or apparently so, usually conspicuously broader than long; synandria 2- to 5-androus, \pm prismatic, truncate at apex; sterile flowers subprismatic, prismatic, lobed, fungiform, or branched (see Sterile Flowers), densely or laxly arranged.

Species list. Species included in *Chlorospatha* sect. *Chlorospatha*: *C. betancurii*, *C. caldasensis*, *C. callejasii*, *C. cedralensis*, *C. chocoensis*, *C. cogolloi*,

C. croatiana, *C. gentryi*, *C. hammeliana*, *C. ilensis*, *C. kolbii*, *C. kressii*, *C. luteynii*, *C. maculata*, *C. mirabilis*, *C. morae*, and *C. risaraldensis* (17 spp., Costa Rica, Panama, northwestern Colombia, and western Ecuador).

Etymology. The type species of the genus, *Chlorospatha kolbii*, is a member of this section.

Discussion. *Chlorospatha* sect. *Chlorospatha* is comprised of 18 of the 19 taxa with divided or deeply lobed leaf blades that are either simple or compound and occurs from Costa Rica southward, through Panama in Central America and northwestern Colombia and western Ecuador in South America and is not known from the eastern slopes of the Andes: *C. betancurii*, *C. caldasensis*, *C. callejasii*, *C. cedralensis*, *C. chocoensis*, *C. cogolloi*, *C. croatiana* subsp. *croatiana*, *C. croatiana* var. *enneaphylla*, *C. gentryi*, *C. hammeliana*, *C. ilensis*, *C. kolbii*, *C. kressii*, *C. luteynii*, *C. maculata*, *C. mirabilis*, *C. morae*, and *C. risaraldensis*. Blades of these taxa are trifid, trisect, pedatifid, or pedatisect. All have sessile stigmas or apparently so (see Style and Stigma Morphology), and all have the same style type (see Style Type 3, Fig. 1), in which the style is expanded into a more or less disklike mantle approximately as broad as the ovary apex.

The combination of sessile stigmas and prominent, disklike styles (Style Type 3) is found exclusively in taxa with divided leaf blades (with leaf segments divided from one another). However, the blade shapes

of two species are intermediate; some collections of each having blades that are not divided are *Chlorospatha hammeliana* and *C. ilensis*. The typical leaf blade of *C. hammeliana* from Panama is ovate-cordate (Fig. 21A); however, one specimen (Croat & Zhu 76881) (Fig. 21C) from an area isolated from the type locality is clearly 3-lobed, whereas the blades of another specimen of the same collection are ovate-cordate. Several collections from that area are intermediate between the typical and 3-lobed forms and some collections from the type locality could also be considered intermediate (Fig. 21B), though less obviously so, these having subhastate blades somewhat less constricted in the area of petiole attachment than those of the 3-lobed specimen and long, prominent posterior lobes, which suggests the possibility that these plants could also eventually consistently or occasionally produce divided blades (with the segments freely separated from one other). The leaf blades of *C. ilensis* can be hastate or even subhastate (Fig. 26B) as well as trifid. Interestingly, numerous collections of *C. ilensis* have been misidentified as *C. mirabile*, the dried blades of the two species often being remarkably similar in shape, with the posterior lobes directed toward the apex and all lobes markedly constricted at their bases, with the laminar tissue frequently only about 1 cm wide between the point of constriction and the posterior rib.

The largest plants in the genus are found in *Chlorospatha* sect. *Chlorospatha*, although most, as for the genus as a whole, are approximately 1 m tall or less. *Chlorospatha croatiana* subsp. *croatiana* and *C. caldasensis* are erect-growing and can be as much as 2 m tall, and several other erect-growing species in this section can be as much as 1.5 m tall. Only 13 taxa of *Chlorospatha* are known to be erect-growing and eight of these are members of *Chlorospatha* sect. *Chlorospatha*, the other five being species in *Chlorospatha* sect. *Occidentales* occasionally reaching 1.5 m tall. Maculate leaf blades occur exclusively in *Chlorospatha* sect. *Chlorospatha*. Taxa in section *Chlorospatha* have three to five erect to erect-spreading leaves; the sympodial leaf is always a fully expanded foliage leaf, and the sides of the petiole sheath are convolute, with the inflorescences held within the sheath and emerging at or near the apex of the sheath. The combination of the somewhat arborescent habit relatively densely arranged pistils, more or less elongated ovaries, disklike styles, and usually broad, prominent, sessile stigmas makes section *Chlorospatha* at least superficially strikingly similar to that found in *Xanthosoma* sect. *Xanthosoma* and suggests possible affinities with that genus. Interestingly, for years, all collections of *C. croatiana*

were misidentified as specimens of *Xanthosoma*, until Grayum's publication of the species in 1986.

Ib. *Chlorospatha* sect. *Occidentales* Croat & L. P. Hannon, sect. nov. TYPE: *Chlorospatha lehmannii* (Engl.) Madison.

Caudex erectus vel decumbens. Folia erecta vel erecto-patentia; lamina integra vel in lobos posteriores divisa. Flos stylo plerumque attenuato in amiculum plus minusve patens expanso, stigmatum plerumque stylo insidente.

Terrestrial or hemiepiphytic, 0.3–1.5 m tall, usually 1 m or less, rarely colonial (*Chlorospatha besseae*); stem usually decumbent, occasionally erect. LEAVES (1)2 to 5, rarely 6 to 8, erect to erect-spreading; sympodial leaf usually a fully expanded foliage leaf, rarely a cataphyll (*C. longiloba*, *C. yatacuensis*); sides of petiole sheath convolute; blades entire and ovate or ovate-elliptic, or simple and sagittate to hastate, rarely trifid (*C. corrugata*), not maculate. INFLORESCENCE with pistils laxly or densely arranged; ovaries approximately as long as wide, plurilocular, rarely semi-unilocular (*C. atropurpurea*, *C. castula*); placentation axile, pseudoaxile, or subaxile, rarely basal (*C. castula*); style expanded into a \pm broadly spreading mantle, usually briefly to prominently attenuate and occupying 1/4 to 2/3 of the length of pistil, rarely obscurely or not at all attenuate (Style Types 4–10); margins conspicuous; stigma \pm elevated on attenuated style, rarely sessile or apparently so, about as broad as long, rarely disklike and wider than long; synandria 2- to 5-androus or occasionally 6-androus, \pm prismatic, truncate at apex.

Species list. Species included in *Chlorospatha* sect. *Occidentales*: *C. amalfiensis*, *C. antioquiensis*, *C. atropurpurea*, *C. bayae*, *C. besseae*, *C. bogneri*, *C. bullata*, *C. caliensis*, *C. carchiensis*, *C. castula*, *C. congensis*, *C. corrugata*, *C. dodsonii*, *C. feuersteiniae*, *C. giraldoi*, *C. grayumii*, *C. hastata*, *C. hastifolia*, *C. huilensis*, *C. jaramilloi*, *C. lehmannii*, *C. litensis*, *C. longiloba*, *C. macphersonii*, *C. mansellii*, *C. munchiquensis*, *C. nambiensis*, *C. narinoensis*, *C. nicolsonii*, *C. noramurphyae*, *C. oblongifolia*, *C. planadensis*, *C. queremalensis*, *C. ricaurtensis*, *C. sagittata*, *C. stellarsarreae*, *C. sucumbensis*, *C. timbiquensis*, *C. tokioensis*, and *C. yatacuensis*.

Etymology. From the Latin “occidentalis,” meaning “western,” referring to distribution confined almost exclusively to the western slopes of the Andes.

Discussion. *Chlorospatha* sect. *Occidentales* consists of 40 species mostly confined to the western slopes of the Andes in Colombia and Ecuador, and

Cordillera Central or Magdalena River drainage region in Colombia.

Chlorospatha huilensis and *C. sucumbensis* are the only species that occur on the eastern slopes of the Andes, in a region where the Cordillera Oriental merges somewhat indistinctly with the Cordillera Central. These two mountain ranges serve as the eastern and western boundaries of the Magdalena River drainage. Maps clearly indicate access from the region of the Magdalena River drainage into the Amazon Basin, where some collections of *C. huilensis* were made, and it is likely that these two species originated in this region rather than in the Amazon drainage (see Geographical Distribution and Endemism). The stylar morphology of these two species, with the style expanded into a mantle, is significantly different from that of all other species from the eastern slopes, all of which have styles lacking mantles.

The style is expanded into a conspicuous, more or less broadly spreading mantle in all species in section *Occidentales* and is more or less attenuated in all but four species: *Chlorospatha castula*, *C. corrugata*, *C. hastata*, and *C. sagittata*. In these four species, the style is obscurely or not at all attenuated and the stigma is actually or apparently sessile, but differs from the style morphology of *Chlorospatha* sect. *Chlorospatha*; the mantle is conspicuously broader than the ovary apex and not at all disklike. Of these four species, only *C. corrugata* is not endemic to Ecuador, occurring instead in northwestern Colombia, significantly distant from the other three species. Additionally, *C. corrugata* is the only member of *Chlorospatha* sect. *Occidentales* with divided leaf blades, these being trifid (i.e., 3-lobed, not divided into segments). *Chlorospatha corrugata* is a 3-lobed species with a style that is expanded into a broadly spreading mantle that is not disklike; therefore, the 3-lobed condition appears to have evolved independently of the other taxa with divided blades, all of which exhibit strong affinities in floral characters. Therefore, *C. corrugata* is a member of *Chlorospatha* sect. *Occidentales*. Comprehensive molecular work has not been done on *Chlorospatha* and would probably be informative in this regard, as would intersectional and interspecific breeding studies.

Otherwise, species in *Chlorospatha* sect. *Occidentales* have three to five erect to erect-spreading leaves with blades that are not divided or maculate and the sympodial leaf is usually a fully expanded foliage leaf, rarely a cataphyll (*C. longiloba*, *C. yatacuensis*). All but four species in *Chlorospatha* sect. *Occidentales* have decumbent stems and most are only occasionally more than 1 m tall. The sides of the

petiole sheath are invariably convolute, regardless of the nature of the sympodial leaf.

The greatest diversity of floral morphology in *Chlorospatha* occurs in *Chlorospatha* sect. *Occidentales*, most significantly in the highly diverse stylar morphology. Seven of the 10 types of styles that occur in the genus are found exclusively in this section (see Style Types 4–10, Fig. 1). Synandria that are 6-androus occur only in *Chlorospatha* sect. *Occidentales*, with *C. ricaurtensis* having 5- to 6-androus flowers (mostly 5-androus), with a few flowers 4-androus, and *C. sagittata* having 4- to 6-androus flowers, with a few flowers 3-androus. Exclusively branched flowers occur in some species of section *Occidentales* and in no taxa in other sections.

Ic. *Chlorospatha* sect. *Orientales* Croat & L. P. Hannon, sect. nov. TYPE: *Chlorospatha longipoda* (K. Krause) Madison.

Caudex decumbens. Folia saepe patentia usque reflexo-patentia vel erecta usque erecto-patentia; lamina integra vel in lobos posteriores divisa. Flores fertiles in synandriis saepe mediano concavis et apicem versus manifeste elongatis, loborum marginibus exterioribus conspicue incrassatis; stylus in amiculum non expansus. Flores steriles prismatici vel subprismatici.

Terrestrial, hemiepiphytic or emergent aquatics, less than 70 cm tall, usually less than 50 cm, frequently colonial; stem usually decumbent, rarely erect. LEAVES several to numerous, 3 to 14, erect to erect-spreading or also spreading to reflexed-spreading in some species; sympodial leaf frequently a cataphyll, occasionally a fully expanded foliage leaf; sides of petiole sheath usually erect, occasionally broadly spreading, rarely convolute; blades entire and narrowly ovate, or simple and sagittate or hastate, not maculate. INFLORESCENCE with pistils \pm densely arranged; ovaries frequently wider than long, plurilocular or unilocular; placentation axile, pseudoaxile, subaxile, sub-basal, or basal; style not expanded into a mantle, usually \pm truncate, rarely briefly attenuate (in 3 species), extremely thin and occupying 1/10 or less of the length of pistil or occupying ca. 1/4 of the length (in attenuated styles); margins usually \pm obscure (Style Types 1, 2); stigma sessile or apparently so, or elevated on style, ca. as broad as long; synandria 2- to 5-androus, usually elongated in direction of axis, twice as long as wide (viewed from above), and broadly concave medially, with margins of lobes prominently thickened, or truncate at apex (in some species); sterile flowers subprismatic or prismatic, densely arranged.

Species list. Species included in *Chlorospatha* sect. *Orientales*: *C. boosii*, *C. cutucuensis*, *C. engleri*, *C. hannoniae*, *C. limonensis*, *C. longipoda*, *C.*

plowmanii, *C. portillae*, *C. pubescens*, *C. sizemoreae*, and *C. yaupiensis*.

None of the species from the Eastern slopes of the Andes, Ecuador, in *Chlorospatha* sect. *Orientales*, have leaf blades that are divided or maculate. The style is not expanded into a mantle and is somewhat obscure, being extremely thin, as broad as or somewhat narrower than the ovary apex, with the margins frequently difficult to discern unless coloration of the style differs from that of the ovary (see Style Type 1, Fig. 1), and in all but three species, the stigma is sessile or apparently so. In *C. cutucuensis*, *C. portillae*, and *C. sizemoreae*, the stigma is elevated on a relatively short, attenuated style that occupies approximately one fourth of the length of the pistil or less (see Style Type 2, Fig. 1). These species also differ from the other members of *Chlorospatha* sect. *Orientales* in having the lower leaf blade surface smooth rather than reticulate, and in *C. cutucuensis* and *C. portillae*, the surface is not narrowly colliculate along all venation as it is in the remaining species. Additionally, these three species, as well as *C. engleri* and *C. limonensis*, have synandria that are more or less truncate at the apex, similar to those found in most other *Chlorospatha*. The unusual synandria found only in the remaining six species are more or less elongated in the direction of the axis, frequently markedly so, broadly concave medially and irregularly lobed, with the outer margins of the lobes moderately to prominently thickened and conspicuously sinuate-undulate, interlocking with the margins of adjacent flowers.

Several additional unusually expressed characters are found exclusively, or nearly so, in species of *Chlorospatha* sect. *Orientales*. All but three species have ovaries that are somewhat broadly cylindrical or obtusely obconical, frequently almost twice as wide as long, obtusely truncate at the apex and frequently also somewhat broadly concave medially. *Chlorospatha* in

other sections have ovaries that are about as long as wide or in some taxa in *Chlorospatha* sect. *Chlorospatha*, longer than wide. Obconical ovaries have been observed only in *Chlorospatha* sect. *Orientales*. Unilocular ovaries occur exclusively in *Chlorospatha* sect. *Orientales*, with exclusively 1-locular ovaries observed in only two collections (*Plowman et al.* 3979 and *Croat et al.* 88008A) of one species, *C. plowmanii*, although a semi-unilocular condition at the apex was reported for *C. castula* and *C. atropurpurea* (in *Chlorospatha* sect. *Occidentales*) by Madison (1978, 1981). In the remaining species with some unilocular ovaries in *Chlorospatha* sect. *Orientales*, most ovaries are 2-locular, with 1-locular ovaries occurring only at the base of the spadix or occasionally interspersed with 2-locular ovaries.

Most species in this section are relatively small plants no more than 50 cm tall, usually colonial, and all have decumbent stems except *Chlorospatha cutucuensis*. Four species, *C. boosii*, *C. hannoniae*, *C. plowmanii*, and *C. pubescens*, have numerous leaves (eight to 14) that are typically spreading to reflexed-spreading as well as erect to erect-spreading. All other taxa of *Chlorospatha* have approximately five or fewer leaves that are exclusively erect to erect-spreading. Leaves are not maculate, and in seven of the 11 species in *Chlorospatha* sect. *Orientales*, the sympodial leaf is a cataphyll, an unusual state that occurs only in two species not in this section (*C. longiloba*, *C. yatacuensis*). The sides of the petiole sheath are rarely convolute in *Chlorospatha* sect. *Orientales* and are usually more or less erect or, as in *C. boosii* and *C. hannoniae*, broadly spreading, thus appearing winged, a condition found in no other taxon in the genus.

Etymology. From the Latin “orientalis,” meaning “eastern,” referring to the distribution of these species exclusively on the eastern slopes of the Andes.

KEY TO SPECIES OF *CHLOROSPATA*

- 1a. Species from Central America.
 - 2a. Leaf blades simple, ovate, cordate to sagittate at base; Panama (Coclé), 710–1150 m *C. hammeliana* Grayum & Croat
 - 2b. Leaf blades with 3 or more lobes.
 - 3a. Leaf blades with 3 lobes, lacking auricles.
 - 4a. Leaf blades usually maculate, drying weakly to moderately bicolorous, weakly glossy to semiglossy and \pm purple, purple-tinged, or purple-mottled abaxially; petiole matte to weakly glossy, the free portion flattened adaxially, usually with acute margins, sheathed 1/2 to 2/3 of its length; Panama (Darién), 550–1400 m *C. mirabilis* (Mast.) Madison
 - 4b. Leaf blades lacking maculations, drying markedly bicolorous, glossy, green abaxially; petiole semiglossy, the free portion \pm terete, sheathed 1/6 to 1/4 of its length; Panama (Veraguas), 800–1030 m *C. hammeliana* Grayum & Croat
 - 3b. Leaf blades with 3 to 5 lobes and moderately to prominently auriculate or \pm rounded at the base on outermost segments or with 5 to 7 lobes and \pm acute at the base, lacking auricles.
 - 5a. Leaf blades with 3 to 5 lobes and moderately to prominently auriculate or \pm rounded at the base; segments broad, broadly attached at the base; primary lateral veins 5 to 7 pairs, arising at 35°–

- 60°; Costa Rica (Heredia, Limón, Puntarenas), 200–750 m; Panama (widespread), 200–1400 m
..... *C. croatiana* Grayum subsp. *croatiana*
- 5b. Leaf blades with 5 to 7 lobes, \pm acute at base, lacking auricles; segments narrow, narrowly attached at base; primary lateral veins 2 to 4 pairs, arising at 15°–35°; Panama (Chiriquí, Coclé, Panamá, Veraguas), 710–1135 m *C. croatiana* var. *enneaphylla* Grayum
- 1b. Species from South America.
- 6a. Species of Magdalena River drainage, occurring on western slopes of Cordillera Oriental, eastern slopes of Cordillera Occidental, and on both slopes of Cordillera Central in Colombia, rarely in Amazon drainage (not occurring on western slopes of Cordillera Occidental in Colombia or western slopes of Andes in Ecuador).
- 7a. Leaf blades simple, sagittate, with posterior lobes directed toward the base.
- 8a. Spathe tube green; spadix adnate to spathe entire length of pistillate portion; sterile staminate portion comprising 1/10 of total length; style broadly spreading, not appressed to ovary; synandria 3- to 4-androus; sterile flowers densely arranged in 3 to 5 whorls.
- 9a. Leaf blades drying matte to weakly glossy, yellow-brown on lower surface, with all but reticulate venation \pm raised and granular-puberulent; primary lateral veins 3 to 5 pairs; peduncle less than 15 cm long; style comprising 1/2 of the length of pistil; Colombia (Huila, Putumayo, sometimes also in Amazon drainage), 2000–2420 m
..... *C. huilensis* Croat & L. P. Hannon
- 9b. Leaf blades drying semiglossy, yellow-green on lower surface, with all venation \pm flattened and glabrous; primary lateral veins 4 to 7 pairs; peduncle more than 20 cm long; style comprising 1/3 of the length of pistil; Colombia (Antioquia), 1800–3000 m
..... *C. antioquiensis* Croat & L. P. Hannon
- 8b. Spathe tube purplish brown; spadix adnate to spathe 1/3 of the length of pistillate portion; sterile staminate portion comprising 1/4 of total length; style not broadly spreading, appressed to ovary; synandria 3-androus; sterile flowers laxly arranged in 9 whorls; Colombia (Antioquia), 1200–1300 m *C. amalfiensis* Croat & L. P. Hannon
- 7b. Leaf blades with 3 or more lobes to palmatisect, with segments directed toward apex.
- 10a. Leaf blades deeply 3-lobed to trisect.
- 11a. Leaf blades with lateral lobes both narrower than and usually shorter than medial lobe; all venation glabrous on lower surface; major venation drying darker than surface; tertiary and reticulate venation \pm obscure; petiole glabrous, sheathed ca. 1/2 of its length; peduncle 42–46 cm long, more than 1/2 as long as petiole.
- 12a. Segments long-acuminate at apex, drying weakly glossy, green on upper surface, with pale maculations; major and secondary venation drying moderately darker than lower surface; spathe tube green; spadix less than 6.5 cm long; fertile staminate portion brown; Colombia (Antioquia), 1550–1850 m *C. betancurii* Croat & L. P. Hannon
- 12b. Segments acute at apex, drying matte, yellowish brown on upper surface, with maculations lacking; major and secondary venation drying markedly darker than lower surface, almost black; spathe tube purple; spadix more than 8 cm long; fertile staminate portion white; Colombia (Antioquia), 1710–1900 m ... *C. callejasii* Croat & L. P. Hannon
- 11b. Leaf blades with lateral lobes both broader than and usually as long as or longer than medial lobe; all venation \pm puberulent on lower surface; major venation drying \pm concolorous; tertiary and reticulate venation conspicuously raised or prominulous; petiole \pm puberulent, sheathed 1/4 to 1/3 of its length; peduncle 3–13 cm long, less than 1/4 as long as petiole; Colombia (Antioquia), 890–1350 m *C. corrugata* Bogner & Madison
- 10b. Leaf blades with 5 or more lobes to palmatisect.
- 13a. Leaf blades with 5 lobes to palmatisect; occurring above 2000 m.
- 14a. Leaf blades with segments free to the base or alate between segments, the confluent portion no more than 1 mm wide, drying matte to weakly glossy on lower surface; petiole sheathed ca. 3/4 of its length; peduncle ca. 60 cm long, almost as long as petiole; Colombia (Risaralda), 2200–2300 m *C. cedralensis* Croat & L. P. Hannon
- 14b. Leaf blades broadly confluent between segments, the confluent portion 1.5–4 cm wide, drying semiglossy to glossy on lower surface; petiole sheathed ca. 1/2 of its length; peduncle 20–43 cm long, ca. 1/2 as long as petiole.
- 15a. Leaf blades brown when fresh, drying moderately bicolorous; primary lateral veins 7 to 8 pairs on innermost lateral segments; petioles brown when fresh, drying semi-intact, \pm fibrous, medium-dark brown; epidermis not separating; spathe tube green, blade white; Colombia (Caldas), 2250 m *C. caldasensis* Croat & L. P. Hannon
- 15b. Leaf blades green when fresh, drying weakly bicolorous; primary lateral veins 4 to 5 pairs on innermost lateral segments; petioles green when fresh, drying intact, almost black, with epidermis in part separated from main body of petiole, glossy, semi-transparent; spathe tube and blade entirely pale green; Colombia (Antioquia; possibly Risaralda), 2440–2800 m *C. luteynii* Croat & L. P. Hannon
- 13b. Leaf blades with 7 to 9 lobes; occurring below 1000 m; Colombia (Antioquia, Boyacá, Chocó), 150–820 m *C. croatiana* var. *enneaphylla* (Grayum) Croat & L. P. Hannon
- 6b. Species of eastern slopes of Andes and Amazon drainage or mostly western slopes of Cordillera Occidental in Colombia and western slopes of Andes in Ecuador.

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- 16a. Species mostly of western slopes of Cordillera Occidental in Colombia and western slopes of Andes in Ecuador.
- 17a. Leaf blades with 3 or more divisions or lobes.
- 18a. Leaf blades with 3 lobes.
- 19a. Leaf blades with lateral lobes both broader than and usually as long as or longer than medial lobe.
- 20a. Leaf blades with all venation drying glabrous and \pm flattened on lower surface, much darker than surface; petiole glabrous, sheathed ca. 1/2 or more of its length, drying dark blackish brown; peduncle glabrous, more than 34 cm long; Colombia (Risaralda), 1500–1550 m *C. risaraldensis* Croat & L. P. Hannon
- 20b. Leaf blades with all venation drying \pm puberulent and \pm raised on lower surface, concolorous to weakly darker than surface; petiole entirely or in part \pm puberulent, sheathed 1/4 to 1/3 of its length, drying medium to medium-dark brown; peduncle granular-puberulent, 3–13 cm long; Colombia (Antioquia), 890–1350 m *C. corrugata* Bogner & Madison
- 19b. Leaf blades with lateral lobes narrower and usually shorter than medial lobe.
- 21a. Species occurring above 1200 m; leaf blades thin; major and secondary veins drying \pm raised on lower surface; petiole sheathed 3/4 or more of its length; sterile staminate portion comprising ca. 1/10 of the length of spadix, with flowers densely arranged; Colombia (Antioquia), 1250–1800 m ... *C. cogolloi* Croat & L. P. Hannon
- 21b. Species occurring below 1000 m; leaf blades thinly coriaceous to subcoriaceous; major and secondary veins drying \pm flattened on lower surface; petiole sheathed 1/3 to 2/3 of its length; sterile staminate portion comprising 1/4 or 2/3 of the length of spadix, with flowers laxly arranged.
- 22a. Leaf blades green on both surfaces; upper surface matte, flat (not quilted); all lobes broadly concave (on mature specimens); primary lateral veins 7 to 10 pairs on lateral segments of mature specimens, aggregated toward base; petiole green, brittle; Colombia (Chocó), 240–825 m *C. maculata* Croat & L. P. Hannon
- 22b. Leaf blades weakly glossy to glossy, green on upper surface, purple to purple-tinged on lower surface; upper surface quilted; all lobes broadly convex; primary lateral veins usually 5 to 6 pairs (rarely 7) on lateral segments of mature specimens, evenly distributed; petiole purple to purplish, spongy.
- 23a. Leaf blades with all segments broadly confluent at base; confluent portion 3.5–4 cm wide; posterior rib not naked; petiole sheathed ca. 1/3 of its length; peduncle less than 20 cm long; sterile staminate portion comprising ca. 1/4 of the length of spadix, the flowers broadly concave medially, fungiform, with undulate margins; Colombia (Chocó), less than 50 m *C. chocoensis* Croat & L. P. Hannon
- 23b. Leaf blades with all segments narrowly confluent at base; confluent portion less than 1 cm wide; posterior rib naked 1–1.5(–2) cm per side; petiole sheathed 1/2 or more of its length; peduncle 30–56 cm long; sterile staminate portion comprising ca. 1/3 of the length of spadix, the flowers obtusely truncate, subprismatic; Colombia (Antioquia, Chocó, Valle), sea level to 150(–900) m *C. mirabilis* (Mast.) Madison
- 18b. Leaf blades with 5 or more lobes.
- 24a. Leaf blades with 5 to 9 segments; segments broadly ovate, elliptical or obovate, to 12 cm wide, less than 4 times longer than wide, \pm acute and free to the base, narrowly attached, moderately inequilateral; spadix sessile.
- 25a. Leaf blades with 5 to 7 segments; all orders of venation crispy-puberulent on lower surface; petiole scurfy-pubescent, sheathed 1/4 to 1/3 of its length; peduncle less than 11 cm long, crispy-puberulent; spathe in part crispy-puberulent abaxially; synandria green; Colombia (Antioquia), 1200–1800 m *C. gentryi* Grayum
- 25b. Leaf blades with 5 to 9 segments; all orders of venation \pm glabrous on lower surface; petiole glabrous, sheathed ca. 1/2 of its length; peduncle 25 cm long, glabrous, striate-ridged; spathe glabrous throughout; synandria white; Colombia (Chocó), 285–825 m *C. morae* Croat & L. P. Hannon
- 24b. Leaf blades with (7 to)9 to 15 segments; segments narrowly elliptical, to 3 cm wide, more than 5 to 10 times longer than wide, broadly attached at base, narrowly confluent between segments, markedly inequilateral; spadix stipitate.
- 26a. Leaf blades velvety on upper surface; spathe more than 7 cm long, green on inner surface; spadix more than 5.5 cm long; axis pale green; sterile staminate spadix ca. 1 cm long or more; Colombia (Chocó), near sea level *C. kolbii* Engl.
- 26b. Leaf blades matte on upper surface; spathe less than 6.5 cm long, dark violet 3/4 of its length on inner surface; spadix less than 5 cm long; axis violet; sterile staminate spadix 4 mm long or less; Colombia (Chocó), less than 500 m *C. kressii* Grayum

- 17b. Leaf blades simple and hastate, sagittate, cordate or cordulate at base.
- 27a. Leaf blades purplish violet-tinged on lower surface.
- 28a. Leaf blades narrowly ovate-sagittate to sagittate; posterior lobes rounded, not acutely pointed at apex; upper surface minutely bullate; all orders of venation prominently raised on lower surface, with sunken areoles; posterior rib not naked; sterile staminate portion comprising ca. 1/10 of total length of spadix, the flowers irregularly lobed; Colombia (Valle), 1020–2000 m *C. bullata* Croat & L. P. Hannon
- 28b. Leaf blades sagittate, sagittate-subhastate, or markedly hastate; posterior lobes acute to acuminate at apex; upper surface \pm smooth (not at all bullate); major, secondary, and tertiary veins weakly to moderately raised or prominulous on lower surface, with areoles lacking; posterior rib naked 1–3.5 cm per side; sterile staminate portion comprising 1/4 to 1/3 of total length of spadix, the flowers fungiform, not lobed.
- 29a. Leaf blades sagittate to occasionally weakly subhastate; anterior and posterior lobes not markedly constricted at base; petiole sheathed 1/2 of its length or more; sheath decurrent at apex; spathe cucullate.
- 30a. Leaf blades with posterior lobes narrow, more than 3 times longer than wide; spathe tube \pm purple; spadix sessile, adnate to spathe most of the length of pistillate portion; style white, broadly spreading, the margins \pm coherent with those of adjacent styles, truncate; stigma sessile; Ecuador (Pichincha), 1200 m *C. castula* (Madison) Madison
- 30b. Leaf blades with posterior lobes broad, less than 2.5 times longer than wide; spathe tube green or cream; spadix stipitate, adnate to spathe only along stipe or occasionally narrowly onto pistillate portion; style orange, appressed to ovary, the margins not coherent with those of adjacent styles, narrowly attenuate; stigma elevated on style; Ecuador (widespread), 100–1200 m *C. atropurpurea* (Madison) Madison
- 29b. Leaf blades hastate to markedly hastate; anterior and posterior lobes markedly constricted at base; petiole usually sheathed less than 1/2 of its length; sheath free-ending at apex; spathe \pm erect; Ecuador (Carchi, Esmeraldas), 375–1800 m *C. hastata* Croat & L. P. Hannon
- 27b. Leaf blades not at all purplish violet-tinged on lower surface.
- 31a. Leaf blades hastate to markedly hastate at base, the posterior lobes prominently spreading.
- 32a. Leaf blades with posterior lobes weakly or not at all constricted at or near base.
- 33a. Petiole sheathed 1/2 of its length (rarely 2/3); leaf blades with posterior lobes broad, less than 2 times longer than wide; peduncle ca. 2/3 as long as petiole; spadix more than 8.5 cm long; sterile flowers densely arranged; Ecuador (Esmeraldas), 647–701 m *C. mansellii* Croat & L. P. Hannon
- 33b. Petiole sheathed 3/4 or more of its length; leaf blades with posterior lobes narrow, more than 2 times longer than wide; peduncle longer than petiole; spadix less than 6.5 cm long; sterile flowers markedly laxly arranged; Colombia (Cauca), ca. 100 m *C. timbiquensis* Croat & L. P. Hannon
- 32b. Leaf blades with posterior lobes markedly constricted near base, the constriction substantially narrower than middle of lobes.
- 34a. Petiole sheathed ca. 1/3 of its length; peduncles less than 20 cm long.
- 35a. Leaf blades drying green, moderately bicolorous; major veins drying mostly weakly paler than lower surface; petiole medium green, with sheath green; fertile staminate spadix cream; sterile staminate spadix less than 9 mm long, the flowers subprismatic to shallowly lobed, densely arranged; Colombia (Nariño), 1100–1325 m *C. narinoensis* Croat & L. P. Hannon
- 35b. Leaf blades drying dark brown to brownish, weakly bicolorous; major veins drying darker than lower surface; petiole pale green, with sheath maroon; fertile staminate spadix brown; sterile staminate spadix more than 1 cm long, the flowers mostly fungiform (like toadstools) to branched, laxly arranged; Colombia (Nariño), 1325 m *C. nambiensis* Croat & L. P. Hannon
- 34b. Petiole sheathed more than 1/2 of its length; peduncles more than 30 cm long.
- 36a. Stems tan or brown, \pm scurfy; petiole smooth, terete or subterete, sheathed 1/2 to 2/3 of its length, \pm purplish to purple-mottled; peduncle 1/2 to 2/3 as long as petiole; style white, cream, or green (rarely weakly orangish yellow-tinged), weakly broader than ovary apex (not broadly spreading), the margins not coherent; stigma sessile or markedly elevated on style; sterile staminate spadix less than 1 cm long, densely flowered.

- 37a. Leaf blades moderately smooth; lower surface not reticulate; spadix less than 10.5 cm long; pistillate portion adnate to spathe 1/3 to 1/2 of its length; style green; stigma sessile; ovaries 2-locular; fertile staminate spadix cream to greenish; Ecuador (widespread), 550–1530 m *C. ilensis* Madison
- 37b. Leaf blades weakly to moderately wrinkled; lower surface conspicuously reticulate; spadix more than 11 cm long; pistillate portion adnate to spathe most or all of its length; style white to cream (rarely weakly orangish yellow-tinged); stigma markedly elevated on style; ovaries 3- to 4-locular; fertile staminate spadix bright orange; Ecuador (widespread), 100–1500 m *C. dodsonii* (G. S. Bunting) Madison
- 36b. Stems dark green or gray-green, smooth; petiole finely many-ribbed, sharply D-shaped with erect, acute margins, sheathed 3/4 or more of its length, \pm entirely dark green; peduncle 3/4 as long as or longer than petiole; style usually orange (rarely white), much broader than ovary apex, the margins \pm coherent; stigma weakly elevated on style; sterile staminate spadix 1.5–2.5 cm long, laxly flowered; Colombia (Nariño), 1100–1325 m; Ecuador (Esmeraldas), 350–425 m *C. litensis* Croat & L. P. Hannon
- 31b. Leaf blades sagittate, subhastate, cordulate to cordate or acute to rounded at base.
 - 38a. Leaf blades cordate to cordulate or rounded to acute at base.
 - 39a. Leaf blades rounded to acute at the base (rarely weakly cordulate).
 - 40a. Petiole sheathed 1/4 to 1/3 of its length; sheath decurrent at apex; leaf blades lanceolate or oblong-elliptic, more than 15 cm long, 3.5 to 5.6 times longer than wide; spadix less than 4 cm long; Colombia (Chocó), 410–465 m *C. oblongifolia* Croat & L. P. Hannon
 - 40b. Petiole sheathed more than 3/4 of its length; sheath free-ending at apex; leaf blades ovate to ovate-elliptic, less than 10 cm long, 1.7 to 1.9 times longer than wide; spadix more than 5 cm long; Colombia (Valle), 2000–2100 m *C. stellasarrae* Croat & L. P. Hannon
 - 39b. Leaf blades cordate to cordulate at base.
 - 41a. Leaf blades moderately smooth, not bullate or rugose; petiole sheathed 1/3 to 2/3 of its length; sheath decurrent at apex.
 - 42a. Leaf blades thin, 12.5–23 \times to 14 cm; upper surface \pm velvety, drying olive-green or dark brown; primary lateral veins less than 7 pairs.
 - 43a. Petiole matte, lacking markings; leaf blades with major veins drying raised on lower surface; tertiary and reticulate veins prominulous; primary lateral veins 4 to 6 pairs; spathe tube entirely matte, pale green to cream; Ecuador (Carchi, Esmeraldas), 550–814 m *C. besseae* Madison
 - 43b. Petiole semiglossy, with weakly darker transverse markings; leaf blades with major veins drying \pm flattened on lower surface; tertiary and reticulate venation obscure; primary lateral veins 3(4) pairs; spathe tube matte, medium green toward base, semiglossy dark purple at apex; Colombia (Nariño), 1100–1130 m *Chlorospatha* sp. indet. 1
 - 42b. Leaf blades subcoriaceous, 38 \times 21.5 cm; upper surface weakly glossy, drying blackened, gray-green; primary lateral veins 8 to 9 pairs; Colombia (Valle), 1250 m *C. queremalensis* Croat & L. P. Hannon
 - 41b. Leaf blades bullate or rugose; petiole sheathed most or all of its length; sheath free-ending at apex.
 - 44a. Leaf blades minutely rugose; spathe less than 9 cm long; spadix less than 7 cm long; fertile staminate spadix bright orange; Colombia (Nariño), 1700–2050 m ... *C. bogneri* Croat & L. P. Hannon
 - 44b. Leaf blades bullate; spathe more than 14 cm long; spadix more than 12 cm long; fertile staminate spadix white; Colombia (Antioquia), 2750–2830 m *C. macphersonii* Croat & L. P. Hannon
- 38b. Leaf blades sagittate or subhastate at base.
 - 45a. Leaf blades sagittate at base; posterior lobes directed toward base or weakly outward (at least on drying).
 - 46a. Species occurring below 900 m.
 - 47a. Leaf blades narrow, more than 2.5 times longer than wide; posterior lobes narrow, more than 2 times longer than wide.

- 48a. Leaf blades narrowly triangular, drying markedly bicolorous; primary lateral veins 4 pairs; Colombia (Valle), 210–230 m *Chlorospatha* sp. indet. 2
- 48b. Leaf blades oblong-elliptic, drying concolorous or weakly to moderately bicolorous; primary lateral veins more than 4 pairs.
- 49a. Petiole sheathed ca. 1/2 of its length; sheath decurrent at apex; free portion subterete, lacking medial keel; primary lateral veins 5 to 6 pairs; inflorescence emerging from sympodial cataphyll; Ecuador (Carchi, Esmeraldas), 300–800 m *C. longiloba* Croat & L. P. Hannon
- 49b. Petiole sheathed ca. 1/3 of its length; sheath free-ending at apex; free portion sharply D-shaped, with low medial keel; primary lateral veins 6 to 9 pairs; inflorescence emerging from apex of petiole sheath; Colombia (Cauca, Chocó), 90–275 m *C. grayumii* Croat & L. P. Hannon
- 47b. Leaf blades broad, less than 2 times longer than wide; posterior lobes broad, less than 1.7 times longer than wide; Colombia (Valle), 700–900 m *C. yatacuensis* Croat & L. P. Hannon
- 46b. Species occurring above 1000 m.
- 50a. Leaf blades \pm bullate or rugose.
- 51a. Leaf blades minutely bullate, with lower surface densely reticulate and areoles deeply sunken, drying green (rarely purplish); Colombia (Valle), 1020–2000 m *C. bullata* Croat & L. P. Hannon
- 51b. Leaf blades weakly bullate (at least on drying) or rugose, with lower surface not densely reticulate, lacking areoles, drying brown.
- 52a. Internodes less than 2 cm long; petiole sheath decurrent at apex; leaf blades weakly bullate and dark purplish brown-speckled on upper surface on drying; anterior lobe more than 2 times longer than posterior lobes; Colombia (Cauca), 1400–1800 m *C. congensis* Croat & L. P. Hannon
- 52b. Internodes 3–4 cm long; petiole sheath free-ending at apex; leaf blades rugose, lacking dark purplish brown speckles on upper surface on drying; anterior lobe less than 1.7 times longer than posterior lobes; Colombia (Cauca), 2580 m ... *C. munchiquensis* Croat & L. P. Hannon
- 50b. Leaf blades \pm smooth, not at all bullate or rugose.
- 53a. Leaf blades with posterior lobes broad, less than 2 times longer than wide.
- 54a. Leaf blades sagittate-subhastate, moderately broadest at base, 1.5 times broader at base than across anterior lobe (measured tip to tip across posterior lobes); spathe tube green; Colombia (Valle), 1400 m ... *Chlorospatha* sp. indet. 3
- 54b. Leaf blades sagittate to ovate-sagittate, weakly broadest at base, 1 to 1.2 times broader at base than across anterior lobe (measured tip to tip across posterior lobes); spathe tube purple.
- 55a. Leaf blades subcoriaceous; most venation drying \pm wrinkled on lower surface; spathe more than 12 cm long; spadix more than 10.5 cm long; Colombia (Valle), 1100–1200 m *C. bayae* Croat & L. P. Hannon
- 55b. Leaf blades thin or thinly coriaceous; all venation drying smooth on lower surface (not wrinkled); spathe less than 12 cm long; spadix less than 9.5 cm long.
- 56a. Petiole sheathed 1/2 of its length, sheath decurrent at apex; peduncle 20 cm long; pistillate portion of spadix adnate to spathe most of its length; stigma elevated on style; sterile flowers densely arranged, branched; Ecuador (Pichincha), 1800–2200 m *C. jaramilloi* Croat & L. P. Hannon
- 56b. Petiole sheathed more than 3/4 of its length; sheath free-ending at apex; peduncle 88 cm

- long; pistillate portion of spadix adnate to spathe ca. 1/2 of its length; stigma sessile; sterile flowers laxly arranged, subprismatic; Ecuador (Imbabura), 1600–1700 m
. *C. sagittata* Croat & L. P. Hannon
- 53b. Leaf blades with posterior lobes narrow, more than 2 times longer than wide.
- 57a. Leaf blades conspicuously narrower at base than across anterior lobe (measured tip to tip across posterior lobes); posterior lobes weakly confluent at base, obscuring petiole apex; posterior rib not naked; Colombia (Chocó), 1000–1900 m *Chlorospatha* sp. indet. 4
- 57b. Leaf blades broadest at base; posterior lobes not confluent at base; posterior rib naked 6–15 mm per side.
- 58a. Leaf blades with anterior and posterior lobes markedly constricted at base on one side; Ecuador (Carchi), 1740–1800 m
. *C. carchiensis* Croat & L. P. Hannon
- 58b. Leaf blades with anterior and posterior lobes weakly or not at all constricted at base.
- 59a. Petiole sheathed less than 1/2 of its length; sheath decurrent at apex; leaf blades drying discolorous, pinkish tan along major veins on lower surface; peduncle less than 14 cm long; spathe less than 8 cm long; Colombia (Valle), 1800–2200 m . . . *C. caliensis* Croat & L. P. Hannon
- 59b. Petiole sheathed 2/3 of its length; sheath free-ending at apex; leaf blades drying brownish green, not at all discolorous; peduncle more than 22 cm long; spathe more than 12 cm long; Colombia (Nariño), 1800–1850 m
. *C. ricaurtensis* Croat & L. P. Hannon
- 45b. Leaf blades subhastate; posterior lobes directed \pm outward (at least on drying).
- 60a. Leaf blade with anterior lobe broadly triangular; posterior lobes broad, less than 1.8 times longer than wide; peduncle more than 48 cm long; spathe tube purple; Colombia (Nariño), 1780–1800 m
. *C. planadensis* Croat & L. P. Hannon
- 60b. Leaf blade with anterior lobe narrowly triangular; posterior lobes narrow, more than 2.5 times longer than wide; peduncle less than 40 cm long; spathe tube cream, yellow, green, or red.
- 61a. Petiole sheathed ca. 1/3 of its length; peduncle less than 16 cm long; spathe less than 10 cm long; spadix less than 8.5 cm long.
- 62a. Internodes short, 1–1.5 cm long; spathe tube green; spathe blade white; sterile staminate portion of spadix less than 2 mm long, laxly flowered; Colombia (Valle, Microndas Tokio), 2000–2100 m *C. tokioensis* Croat & L. P. Hannon
- 62b. Internodes long, 2–4 cm long; spathe entirely cream or yellow; sterile staminate portion of spadix 3–8 mm long, densely flowered; Colombia (Antióquia, possibly also Chocó), 1500–1800 m *C. nicolsonii* Croat & L. P. Hannon
- 61b. Petiole sheathed ca. 1/2 or more of its length; peduncle more than 19 cm long; spathe more than 10 cm long; spadix more than 8.5 cm long.
- 63a. Petiole sheathed ca. 1/2 of its length; sheath free-ending; leaf blades coriaceous, drying densely dark purplish brown-speckled on upper surface, matte on lower surface; spathe tube green; spathe blade white; sterile staminate spadix less than 1 cm long; Colombia (Cauca), 1500–1800 m
. *C. lehmannii* (Engl.) Madison
- 63b. Petiole sheathed 2/3 or 3/4 of its length; sheath decurrent; leaf blades thin or thinly coriaceous, drying without dark purplish brown speckles on upper surface, weakly glossy to semiglossy on surface; spathe entirely \pm yellow or red; sterile staminate spadix more than 1.2 cm long.

- 64a. Petiole sheathed 2/3 of its length or slightly less; posterior lobes markedly narrow, 3.5 to 5 times longer than wide; spathe creamy yellow; fertile staminate spadix creamy yellow; sterile staminate spadix 1.3–1.8 cm long; Colombia (Valle), 1700–2000 m
..... *C. giraldoi* Croat & L. P. Hannon
- 64b. Petiole sheathed ca. 3/4 of its length; posterior lobes moderately narrow, 2.6 to 3.2 times longer than wide; spathe red; fertile staminate spadix pink; sterile staminate spadix 1.8–2.5 cm long; Colombia (Valle), 1700 m
..... *C. noramurphyae* Croat & L. P. Hannon
- 16b. Species of eastern slopes of Andes and Amazon drainage in Colombia and Ecuador.
- 65a. Leaf blades purple on the lower surface; Ecuador (Morona-Santiago, Cordillera de Cutucú), ca. 700 m
..... *C. feuersteiniae* (Croat & Bogner) Bogner & L. P. Hannon
- 65b. Leaf blades green on the lower surface.
- 66a. Style expanded into a mantle, broader than ovary apex.
- 67a. Leaf blades more than 25 cm long, 2.7 times longer than wide; prominently constricted in area of petiole attachment; posterior lobes 3.5 to 3.7 times longer than wide
..... *C. hastifolia* Bogner & L. P. Hannon
- 67b. Leaf blades less than 23 cm long, less than 2 times longer than wide, weakly constricted or not at all constricted in area of petiole attachment; posterior lobes less than 3 cm longer than wide; Colombia (Amazonas), less than 300 m.
- 68a. Style briefly attenuate, comprising 1/3 of the length of pistil, appressed to ovary; petiole sheathed 1/3 of its length; leaf blades drying green; anterior lobe broad, 1.2 times longer than wide; posterior lobes broad, 1.6 times longer than wide; upper surface matte; lower surface reticulate, narrowly colliculate along most veins, the veins drying paler than surface; Ecuador (Sucumbíos), 2200–2350 m
..... *C. sucumbensis* Croat & L. P. Hannon
- 68b. Style long-attenuate, comprising 1/2 of the length of pistil, broadly spreading, not appressed to ovary; petiole sheathed 1/2 of its length; leaf blades drying yellow-brown; anterior lobe narrow, 1.7 to 1.9 times longer than wide; posterior lobes narrow, 2.3 to 2.9 times longer than wide; upper surface semiglossy; lower surface not reticulate and not colliculate along the veins, the veins drying darker than the surface; Colombia (Huila, Putumayo), 2000–2400 m
..... *C. huilensis* Croat & L. P. Hannon
- 66b. Style lacking a mantle, as broad as or narrower than ovary apex.
- 69a. Leaf blades with all venation glabrous on lower surface.
- 70a. Synandria truncate at apex, ± symmetrical, ± prismatic, the lobes not thickened.
- 71a. Leaf blades acute to rounded at base, lacking posterior lobes; sympodial leaf a cataphyll; Ecuador (Zamora-Chinchipe), 900–1455 m
..... *C. portillae* Croat & L. P. Hannon
- 71b. Leaf blades with posterior lobes; sympodial leaf a full expanded foliage leaf.
- 72a. Leaf blades, ovate-elliptic, subsagittate at base; lower surface reticulate; spathe reflexing after anthesis; fertile staminate portion of spadix dark purple; style not attenuate; Ecuador (Morona-Santiago), 1200 m
..... *C. limonensis* Croat & L. P. Hannon
- 72b. Leaf blades sagittate or sagittate-subhastate at base; lower surface not reticulate; spathe erect after anthesis; fertile staminate portion of spadix white or pale greenish yellow; style attenuate.
- 73a. Leaf blades narrow, ca. 3.3 times longer than wide, with anterior lobe long, ca. 3 times longer than posterior lobes; spadix 4.1 cm long, adnate to spathe ca. 2/3 of length of pistillate portion at base; pistils green; ovaries 2- to 3-locular, with 12 to 14 ovules per locule; synandria 2- to 3-androus, pale greenish yellow; Ecuador (Zamora-Chinchipe), 1200–2000 m (est.)
..... *C. sizemoreae* Croat & L. P. Hannon
- 73b. Leaf blades broad, 1.1 to 1.3 times longer than wide with anterior lobe short, ca. 1.5 to 2 times longer than posterior lobes; spadix 6–6.4 cm long, adnate to spathe ca. 1/4 of length of pistillate portion at base; pistils cream to pale yellow; ovaries 3- to 4-locular, with 4 to 10 ovules per locule; synandria 3- to 4-androus, white; Ecuador (Morona-Santiago), 1700–1900 m
..... *C. cutucuensis* Madison
- 70b. Synandria broadly concave medially, ± highly bilaterally symmetrical, ± elongated in direction of axis, with the lobes ± prominently thickened.

- 74a. Leaf blades hastate or subhastate, the posterior lobes directed outward, \pm acute at apex; spathe reflexing after anthesis; Ecuador (Napó, Sucumbíos), 250–1200(–1486) m *C. plowmanii* (Madison) Croat & L. P. Hannon
- 74b. Leaf blades \pm ovate or ovate-elliptic, sagittate or subsagittate at base, the posterior lobes directed toward base, broadly to narrowly rounded at apex; spathe erect after anthesis.
- 75a. Leaves numerous, 8 to 14, erect to reflexed spreading; blades \pm broadly ovate; sides of petiole sheath broadly spreading, appearing winged; cataphylls produced only when in flower, not appressed to petioles, ultimately deciduous.
- 76a. Upper surface of leaf blade sub-bullate, weakly glossy, dark blackish green; posterior lobes decurrent onto petiole; posterior rib not naked; spathe less than 6.5 cm long, the blade dark maroon; style white and densely dark purple-speckled; Ecuador (Morona-Santiago), 940 m *C. hannoniae* Croat
- 76b. Upper surface of leaf blade broadly quilted velvety, medium to dark green; posterior lobes decurrent onto posterior rib, the posterior rib naked 3–9 mm per side; spathe more than 7.5 cm long, the blade green; style pale green to yellow-green; Ecuador (Morona-Santiago), 500–944 m *C. boosii* Croat & L. P. Hannon
- 75a. Leaves several, 3 to 5, erect to erect-spreading; blades ovate-elliptic; sides of petiole sheath erect or in-rolled; cataphylls produced with each vegetative and sympodial length of stem; Ecuador (widespread), (265–)470–1700 m
..... *C. longipoda* (K. Krause) Madison
- 69b. Leaf blades with all or most venation \pm crispy-puberulent to granular-puberulent on lower surface.
- 77a. Stem red; inflorescence emerging from apex of petiole sheath; sympodial leaf a fully expanded foliage leaf; sympodium held within petiole sheath; Ecuador (Morona-Santiago), 1600–1800 m *C. yaupiensis* Croat & L. P. Hannon
- 77b. Stem green; inflorescence emerging from base of petiole sheath; sympodial leaf a cataphyll; sympodium held within sympodial cataphyll.
- 78a. Synandria truncate at apex, the lobes not thickened, \pm symmetrical; leaves erect to erect-spreading; leaf blades triangular-sagittate, bullate on upper surface; spathe, peduncle and cataphyll glabrous; Ecuador (Morona-Santiago), 1659 m *C. engleri* Croat & L. P. Hannon
- 78b. Synandria broadly concave medially, the lobes prominently thickened, highly bilaterally symmetrical, \pm elongated in direction of axis; leaves erect to reflexed-spreading; leaf blades hastate to subhastate, broadly quilted on upper surface, the intervening surface smooth; spathe, peduncle, and cataphyll usually \pm crispy-puberulent; Ecuador (widespread), 400–1551 m *C. pubescens* Croat & L. P. Hannon

KEY TO SPECIES FROM THE FRONTIER REGION ALONG THE BORDER OF COLOMBIA (NARIÑO) AND ECUADOR (CARCHI, ESMERALDAS, SUCUMBÍOS), NOT KNOWN ELSEWHERE IN EITHER COLOMBIA OR ECUADOR

- 1a. Leaf blades cordate to cordulate or subtruncate at base, the width at base less than width of anterior lobe, the base 0.5 to 0.9 times as wide as anterior lobe (measured tip to tip across posterior lobes).
- 2a. Leaf blades \pm smooth, not rugose; petiole sheathed 1/3 to 2/3 of its length; sheath decurrent at apex.
 - 3a. Petiole matte, lacking markings; leaf blades with major veins drying raised on lower surface; tertiary and reticulate venation prominulous; primary lateral veins 4 to 6 pairs; spathe tube matte, pale green to cream; Ecuador (Carchi, Esmeraldas), 550–814 m *C. besseae* Madison
 - 3b. Petiole semiglossy, with weakly darker transverse markings; leaf blades with major veins drying \pm flattened on lower surface; tertiary and reticulate venation \pm obscure; primary lateral veins 3(4) pairs; spathe tube matte, medium green toward base, semiglossy, dark purple at apex; Colombia (Nariño), 1100–1130 m *Chlorospatha* sp. indet. 1
- 2b. Leaf blades minutely rugose; petiole sheathed most or all of its length; sheath free-ending at apex; Colombia (Nariño), 1700–2050 m *C. bogneri* Croat & L. P. Hannon
- 1b. Leaf blades sagittate to hastate at base, the width at the base greater than width of anterior lobe, the base 1.1 to 3.3 times wider than anterior lobe (measured tip to tip across posterior lobes when flattened).
- 4a. Leaf blades with anterior and posterior lobes scarcely or not at all constricted at the base.
 - 5a. Leaf blades hastate to subhastate, the posterior lobes directed outward.
 - 6a. Species occurring only on eastern slopes of Andes, above 2100 m; Ecuador (Sucumbíos), 2200–2350 m *C. sucumbensis* Croat & L. P. Hannon
 - 6b. Species occurring only on western slopes of Andes, below 1900 m.

- 7a. Internodes short, 1–1.5 cm long; leaf blade surfaces matte to weakly glossy; lower surface reticulate; peduncle less than 35 cm long; spathe tube pale green to greenish cream; fertile staminate spadix bright orange; stigma weakly elevated on style; Ecuador (Esmeraldas), 700 m *C. mansellii* Croat & L. P. Hannon
- 7b. Internodes long, 3.5–8 cm; leaf blade surfaces semiglossy; lower surface smooth; peduncle more than 45 cm long; spathe tube dark purple-violet; fertile staminate spadix white or cream; stigma prominently elevated on style; Colombia (Nariño), 1700–1800 m
..... *C. planadensis* Croat & L. P. Hannon
- 5b. Leaf blades sagittate, the posterior lobes directed toward the base.
 - 8a. Petiole purple-tinged, sheathed 2/3 of its length; sheath free-ending at apex; primary lateral veins 3 pairs; spathe more than 12 cm long; spadix more than 11 cm long; stigma weakly elevated on style; sterile staminate spadix more than 1.4 cm long, the flowers mostly branched; synandria 5- to 6-androus, drying dark purplish, almost black; Colombia (Nariño), 1800–1850 m
..... *C. ricourtensis* Croat & L. P. Hannon
 - 8b. Petiole green, sheathed ca. 1/2 of its length; sheath decurrent at apex; primary lateral veins 5 to 6 pairs; spathe less than 9 cm long; spadix less than 6 cm long; stigma prominently elevated on style; sterile staminate spadix less than 1 cm long, the flowers subprismatic; synandria 3- to 4-androus, drying cream-colored; Ecuador (Carchi, Esmeraldas), 300–800 m
..... *C. longiloba* Croat & L. P. Hannon
- 4b. Leaf blades with anterior and posterior lobes markedly constricted at base, at least on one side.
 - 9a. Leaf blades sagittate, the posterior lobes directed toward the base; Ecuador (Carchi), 1740–1800 m
..... *C. carchiensis* Croat & L. P. Hannon
 - 9b. Leaf blades markedly hastate, the posterior lobes directed outward.
 - 10a. Leaf blades ± dark purple-mottled on lower surface; Ecuador (Carchi, Esmeraldas), 375–1800 m
..... *C. hastata* Croat & L. P. Hannon
 - 10b. Leaf blades not at all purplish on lower surface.
 - 11a. Leaf blades with upper surface corrugate; petiole sheathed 3/4 or more of its length; peduncle more than 35 cm long, more than 3/4 as long as to longer than petiole; spadix more than 8 cm long; fertile staminate portion orange; sterile staminate portion long, 1.5–2.5 cm long; stigma weakly elevated on style; Colombia (Nariño); Ecuador (Esmeraldas), 425–1325 m
..... *C. litensis* Croat & L. P. Hannon
 - 11b. Leaf blades with upper surface ± smooth, not corrugate; petiole sheathed less than 1/2 of its length; peduncle less than 18 cm long, ca. 1/2 as long as petiole; spadix less than 6.5 cm long; fertile staminate portion cream or brownish; sterile staminate portion short, 0.5–1.1 cm long; stigma markedly elevated on style.
 - 12a. Leaf blades drying green; major venation drying weakly paler than lower surface; petiole sheath green; fertile staminate spadix cream-colored; sterile flowers irregularly subprismatic, densely arranged; Colombia (Nariño), possibly Ecuador (Carchi), 800–1325 m
..... *C. narinoensis* Croat & L. P. Hannon
 - 12b. Leaf blades drying brown; major venation drying conspicuously darker than lower surface; petiole sheath maroon; fertile staminate spadix brownish; sterile flowers fungiform to branched, laxly arranged; Colombia (Nariño), 1150–2900 m
..... *C. nambiensis* Croat & L. P. Hannon

1. *Chlorospatha amalfiensis* Croat & L. P. Hannon, Aroideana 27: 3. 2004. TYPE: Colombia. Antioquia: along Amalfi–Fraguas rd., NE of Salazar, 23–26.5 km from center of Amalfi, 1220–1300 m, 6°58'N, 74°59'W, 14 Feb. 1989, *J. MacDougal, J. Betancur, W. J. Kress & B. Echeverry* 4034 (holotype, HUA!). Figure 4C.

Terrestrial herb, ca. 50 cm tall; stem (possibly decumbent) length not known, remnants of old cataphylls persisting ± intact at upper nodes (all measurements made from dried material); internodes 1–1.5 × 1.2–1.5 cm, drying matte, medium grayish brown, prominently wrinkled; cataphylls ca. 20 cm long, acuminate at apex, drying semiglossy, dark reddish brown. LEAVES 5, erect-spreading; **petioles** 36–37 cm long, drying glabrous, matte to weakly glossy, dark reddish brown, sheathed 20–24 cm (8–

12 cm on foliage leaves), ca. 1/2 of total length; sheath decurrent at apex; free portion 2–2.5 mm diam. midway; **blades** sagittate, 19–21 × 11–11.5 cm (9.8–10 cm wide at base, measured tip to tip across posterior lobes), 1.7 to 1.8 times longer than wide, long-acuminate at apex, broadest across anterior lobe, drying thin, weakly bicolorous; upper surface drying matte to weakly glossy, dark yellow-brown, weakly grayish; lower surface drying weakly glossy to semiglossy; anterior lobe 14.5 × 11–11.5 cm, 1.3 times longer than wide, 1.8 to 2 times longer than posterior lobes, broadest near base, ± symmetrical; posterior lobes directed toward base, 7–8 × 5.2–5.8 cm, 1.3 to 1.4 times longer than wide, narrowly rounded to bluntly acute at apex, broadest at base, prominently inequilateral, the inner side narrower, ± acute and narrowly confluent with opposite lobe at

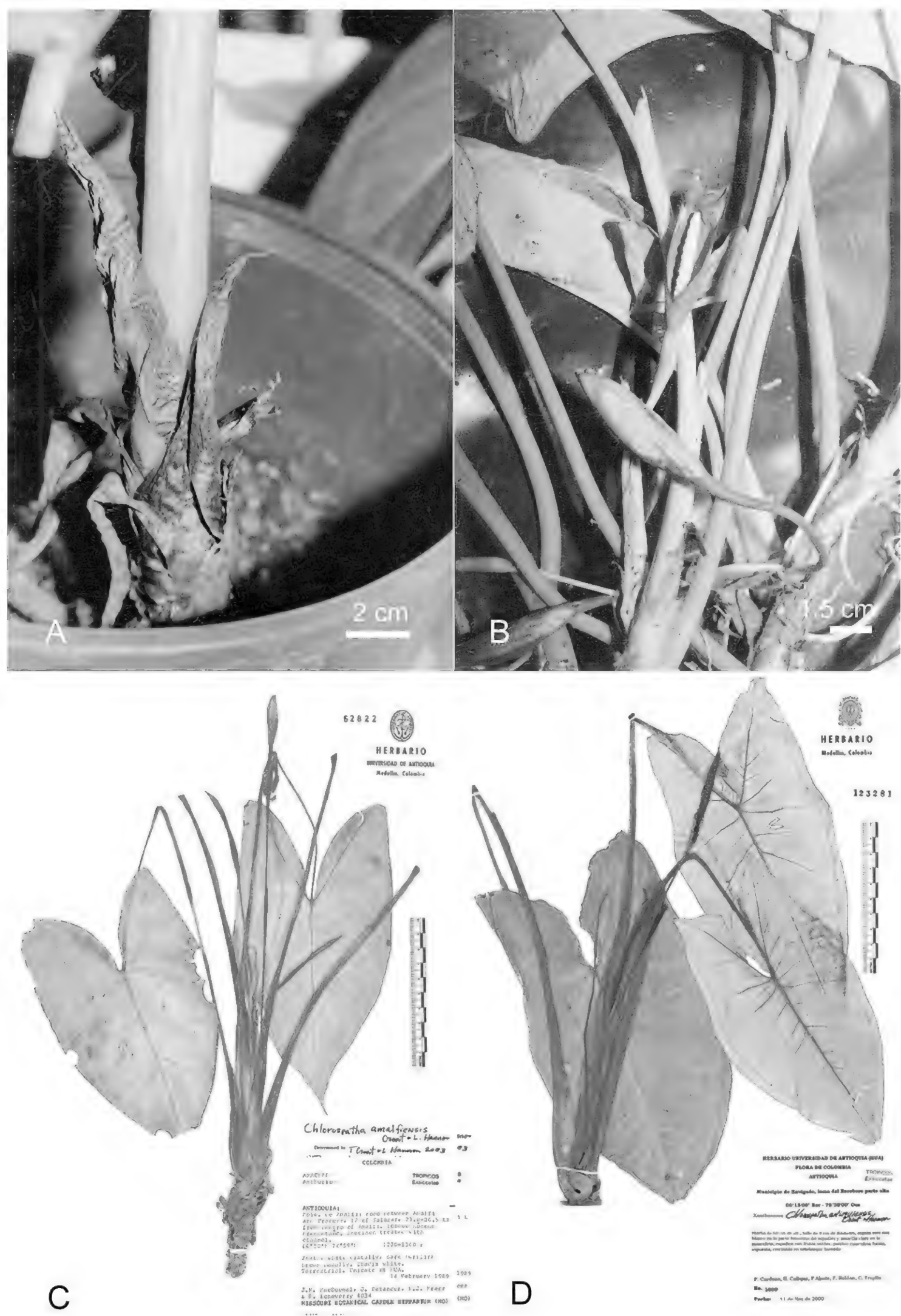


Figure 4. —A. *Chlorospatha hammeliana* Grayum & Croat, stem with dried cataphylls, *Croat* 44589 (MO). —B. *Chlorospatha longipoda* (K. Krause) Madison, stem with both inflorescence at anthesis and mature infructescence, *Croat et al.* 86561 (MO). —C. *Chlorospatha amalfiensis* Croat & L. P. Hannon, *MacDougal et al.* 4034I (HUA holotype). —D. *Chlorospatha antioquiensis* Croat & L. P. Hannon, *Cardona et al.* 1050 (HUA).

base, the confluent portion obscuring petiole apex; outer side 3.4 to 4.5 times wider than inner side midway; midrib and major veins drying weakly raised to flattened on lower surface, moderately darker than surface; **basal veins** 6, first free to the base, 5 coalesced into a prominent posterior rib, 3 acroscopic, 2 basiscopic; primary lateral veins 2 pairs, arising at 25° – 32° , weakly arcuate; secondary veins drying weakly raised on lower surface, weakly darker than surface; tertiary veins drying flattened on lower surface, weakly darker than surface; reticulate veins drying obscure on lower surface, in part weakly darker than surface; collective veins 3, the innermost arising from lowermost lateral vein on inner side of posterior lobe, \pm parallel to and ca. 6 mm from margin. **INFLORESCENCES** erect, 5 per axil; peduncle held within the sheath, 18–23 cm \times 1–1.5 mm, drying matte to weakly glossy, dark brown; **spathe** erect, 7–7.5 cm long, cuspidate at apex; spathe tube purplish brown on outer surface, 3.8 cm \times 4.5–5 mm, drying matte, dark brown on outer surface; spathe blade white, 3.7 cm \times 4–4.5 mm, drying matte, medium reddish brown on outer surface, paler on inner surface, marcescent, erect after anthesis; **spadix** erect, 5.7 cm long, sessile, adnate to spathe 8 mm at base, ca. 1/3 of the length of pistillate portion; pistillate portion 2.2 cm \times 3 mm, drying brownish; fertile staminate portion 1.8–1.9 cm \times 3 mm, clavate, narrowly rounded at apex, drying medium dark brown; sterile staminate portion 1.3 cm \times 1.5 mm, \pm cylindrical, drying tan; pistils laxly arranged, ca. 3 across the axis (viewed from above), ca. 1.5–2 mm long; ovaries subglobose, ca. 1 \times 1–1.5 mm, drying dark brown; style Type 8 (Fig. 1), 0.7–1 \times ca. 1.5 mm, comprising 1/2 of the length of pistil, the margins weakly coherent with those of adjacent styles; **stigma** elevated on and weakly broader than narrowed portion of style, ca. 0.3 mm diam., drying dark brown; synandria ca. 1 \times 1–1.2 mm, coherent, truncate, 3-lobed, 3-androus; sterile flowers ca. 1 \times 1 mm, subprismatic to irregularly lobed, laxly arranged, in 9 whorls. Berries not known.

Phenology. Flowering is only known to occur in *Chlorospatha amalfiensis* during the month of February.

Discussion. *Chlorospatha amalfiensis* is known only from the type and is endemic to the eastern slopes of the Cordillera Central in Antioquia Department, Colombia, at 1200–1300 m elevation. The species was collected in tropical wet forest and would be expected to occur elsewhere in that department. The species is a member of *Chlorospatha* sect. *Occidentales* and distinguished by its ovate-

sagittate leaf blades that are narrower at the base than across the anterior lobe and dry grayish yellow-brown on the upper surface, with the inner margins of the posterior lobes narrowly confluent at the base, obscuring the petiole apex. It is also distinguished by its purplish brown spathe tube, white spathe blade, and short spadix (5.7 cm long), with the sterile portion comprising about one fourth of its length and the sterile flowers laxly arranged. The fertile staminate portion is clavate, with the synandria unusual in being strictly 3-androus.

Chlorospatha amalfiensis could be confused with only one species, *C. antioquiensis*, which also occurs on the eastern slopes of the Cordillera Central but at higher elevations, 1800–3000 m. The petiole of the latter species dries with the epidermis partially separated intact and semiglossy, with the sheath free-ending at the apex, differing from that of *C. amalfiensis*, which dries matte, with the sheath decurrent and the epidermis not separated. The leaf blade of the latter species has two pairs of primary lateral veins and dries more or less yellow-brown, whereas that of *C. antioquiensis* has four to seven pairs of primary lateral veins and dries greenish. The spathe tube of *C. antioquiensis* is green and the blade green or yellow, thus differing from *C. amalfiensis*, which has a purplish brown tube and white blade. The spadix of the latter species is adnate to the spathe only one third of the length of the pistillate portion and has somewhat laxly arranged pistils and a Type 8 style (Fig. 1) that comprises one half of the length of the pistil, whereas the spadix of *C. antioquiensis* is adnate to the entire length of the pistillate portion and has comparatively densely arranged pistils and a Type 6 style (Fig. 1) that comprises one third of the length of the pistil. The fertile staminate portion is cylindrical to tapering in the latter species, with the synandria 3- to 4(5)-androus, whereas that of *C. amalfiensis* is clavate, with the synandria no more than 3-androus. The sterile staminate portion comprises one fourth of the length of the spadix in the latter species, with the sterile flowers laxly arranged, whereas that of *C. antioquiensis* comprises one tenth of total length, with the sterile flowers densely arranged.

2. *Chlorospatha antioquiensis* Croat & L. P. Hannon, *Aroideana* 27: 6. 2004. TYPE: Colombia. Antioquia: along Medellín–Sonsón rd., 5–6 km SE of La Unión, 2400 m, 26 Mar. 1979, J. Luteyn & M. Luteyn 7110 (holotype, NY!; isotype, COL!). Figure 4D.

Terrestrial or hemiepiphytic herb, 50–60 cm tall; stem decumbent, at least 20 cm long, remnants of old

leaf bases and cataphylls persisting intact along its length (all measurements made from dried material); internodes 1.5–3 × 0.6–1.3(–4) cm, drying weakly glossy, dark brownish green; cataphylls 11–24 cm long, obtuse with acumen at apex, drying weakly glossy to semiglossy, medium to dark reddish brown. LEAVES 2 to 4, erect-spreading; **petioles** 29–52 cm long, drying glabrous, weakly glossy to semiglossy, medium-dark to dark reddish brown or almost black, with epidermis in part separated ± intact and semi-transparent, sheathed 17–31 cm, slightly more than 1/2 of total length; sheath free-ending at apex; free portion 2–5 mm diam. midway; **blades** sagittate and broadly triangular or ovate-sagittate, (16.5–)20–26 × 8.5–14.5 cm, 1.9 to 2.2 times longer than wide, gradually to scarcely acuminate at apex, occasionally abruptly acuminate, usually broadest at base, rarely weakly narrower, (0.8 to)1.1 times wider at base than across anterior lobe (measured tip to tip across posterior lobes), weakly or not at all constricted in area of petiole attachment (at least on one side), drying thin, weakly to moderately bicolorous, occasionally concolorous; upper surface drying matte, medium to dark yellow-green to olive-green; lower surface drying semiglossy to glossy; anterior lobe (11–)14–17 × (7.5–)9–14.5 cm, 1.1 to 1.5 times longer than wide, 1.4 to 1.9 times longer than posterior lobes, broadest near base, ± symmetrical; posterior lobes directed toward base or weakly outward, (6.1–)7.3–11 × (3.2–)4–6.8 cm, 1.5 to 1.9 times longer than wide, bluntly acute to narrowly rounded at apex, rarely bluntly rounded, weakly broader midway than at base, weakly inequilateral, the inner side narrower, rounded at base, briefly attenuate and usually weakly confluent with opposite lobe, the confluent portion obscuring petiole apex; outer side ± straight toward base; midrib and major venation drying ± flattened on lower surface, usually moderately darker to much darker than surface, rarely weakly darker; midrib round-raised on lower surface; **basal veins** 3 to 5 pairs, coalesced into a prominent posterior rib; primary lateral veins 4 to 7 pairs, arising at 50°–65°(–90°), weakly arcuate or straight, convex on lower surface; secondary veins drying in part weakly raised or prominulous on lower surface, otherwise ± flattened, in part concolorous, otherwise weakly darker than surface; tertiary veins drying visible, ± flat on lower surface, in part weakly darker than surface, otherwise concolorous; reticulate veins drying in part visible on lower surface; collective veins 3, the innermost arising from apex of posterior rib or from one of the lateral veins on inner side of posterior lobe, ± parallel to margin, occasionally moderately scalloped, 4–6(–12) mm

from margin. INFLORESCENCES erect, 2 per axil; peduncle held within the sheath, (21–)26–29 cm × ca. 2 mm, drying matte to weakly glossy, medium-dark brown; **spathe** erect, 7.2–9 cm long, abruptly acuminate at apex; spathe tube medium or pale green on outer surface, 2.8–4 cm × 3–5 mm, drying matte, dark reddish brown on outer surface, weakly glossy and paler on inner surface; spathe blade green or yellow, 4.5–6 cm × 5–7 mm (ca. 2 cm wide when flattened), drying matte, pale to medium reddish tan on both surfaces, marcescent, erect after anthesis; **spadix** erect, (6–)6.5–8.4 cm long, sessile, adnate to spathe 2.6–3 cm at base, the entire length of pistillate portion; pistillate portion green or white, 2.6–3 cm × 2.5–3.5 mm, drying reddish brown; fertile staminate portion red, yellow, or green, 3–5.1 cm × 3–6 mm, cylindrical or tapering, frequently curving forward, acute to narrowly rounded at apex, drying dark reddish brown; sterile portion 7–10 × 2–4 mm, broadest at apex, rarely broadest at base, with axis naked 1–1.5 mm at base, drying medium reddish brown; pistils weakly coherent, 3 to 4 across the axis (viewed from above), ca. 2 mm long; ovary subglobose, 1–1.5 × 1.5–2 mm, drying creamy tan with darker veins; style Type 6 (Fig. 1), ca. 0.6 × ca. 2 mm, comprising ca. 1/3 of the length of pistil (attenuate portion less than 0.5 mm long), the margins weakly coherent with those of adjacent styles; **stigma** weakly elevated on and drying weakly broader than narrowed portion of style; synandria 1–1.5 × 1–1.5 mm, coherent, truncate, 3- to 4(5)-lobed, mostly 3- to 4-androus; sterile flowers 1–1.5 mm long, 1.5–2 × 1–1.5 mm diam. and ± elongated in direction of axis, coherent, truncate, irregularly subprismatic, in ca. 5 whorls. Berries green.

Phenology. Flowering is only known to occur in *Chlorospatha antioquiensis* in March, April, October, and November.

Discussion. *Chlorospatha antioquiensis* is endemic to the eastern and western slopes of the Cordillera Central in Antioquia Department, Colombia, to the north and south of Medellín, at 1800–3000 m elevation, 3000 m being the highest elevation recorded for the genus. It occurs on the borders of four life zones, premontane rainforest, lower montane rainforest, premontane moist forest, and premontane wet forest, also in premontane wet forest or possibly either lower montane wet forest or premontane moist forest. The species is a member of *Chlorospatha* sect. *Occidentales* and is distinguished by its sagittate leaf blades that dry matte on the upper surface, more or less glossy on the lower surface, with the inner margins of the posterior lobes weakly confluent at the

base, obscuring the petiole apex, and by its red, yellow, or green synandria, a range of coloration unique in the genus. Consequently, the possibility that more than one species is involved was considered. All collections examined proved to be virtually identical in all other respects, both floral and vegetative, and, therefore, were determined to be representative of the same species.

Chlorospatha antioquiensis could be easily confused with only one species, *C. amalfiensis*, which also occurs on the eastern slopes of the Cordillera Central, but at lower elevations, 1220–1300 m (see discussion under *C. amalfiensis*).

Chlorospatha antioquiensis could possibly be confused with *C. huilensis* from the Magdalena River drainage in Huila and Putumayo departments, Colombia. In the latter species, the leaf blade dries yellow-brown and has three to five pairs of primary lateral veins and most venation granular-puberulent and raised on the lower blade surface, whereas the blade of *C. antioquiensis* dries yellow-green and has four to seven pairs of primary lateral veins and all venation glabrous and more or less flattened. The petiole of *C. antioquiensis* dries with the epidermis partially separated more or less intact from the main body and semiglossy to glossy, whereas that of *C. huilensis* dries weakly glossy, with the epidermis not separated. The peduncle is more than 20 cm long and the style is Type 6 (Fig. 1) in the latter species, whereas in *C. huilensis*, the peduncle is less than 15 cm long and the style is Type 5 (Fig. 1), in plants of comparable size.

Chlorospatha antioquiensis could be confused with *C. jaramilloi*, particularly in the sterile state, but the latter species is known only from Pichincha Province, Ecuador, on the western slopes of the Andes. The most significant differences between the species are found in the inflorescences. The spathe tube is purple and the blade cream-colored in *C. jaramilloi*, whereas in *C. antioquiensis*, the tube is green and the blade, yellow or green. The style is Type 6 (Fig. 1) in *C. antioquiensis* and Type 5 (Fig. 1) in *C. jaramilloi*. The fertile staminate spadix of *C. antioquiensis* is red, yellow, or green and either tapering or cylindrical, whereas that of *C. jaramilloi* is cream-colored and ellipsoid. The sterile flowers of *C. antioquiensis* are subprismatic, differing from the conspicuously 2- to 6-branched flowers found in *C. jaramilloi*.

Additional specimens examined. COLOMBIA. **Anti-óquia:** Mpio. Sonsón, via Sonsón–La Soledad, rd. to Río Verde de los Montes, end of La Palmita–Río Verde de los Montes trail, Paramo de los Palomas, 3000 m, *R. Callejas et al.* 6408 (HUA); Mpio. Yarumal, El Cedro trail, along rte. from Alto de Ventanas to El Cedro, 127 km NE of Medellín, 1600–1800 m, *R. Callejas et al.* 10815 (HUA); Mpio.

Envigado, high part of Escobero hill, *F. Cardona et al.* 1050 (HUA).

3. *Chlorospatha atropurpurea* (Madison) Madison, Selbyana 5(3–4): 354. 1981. Basionym: *Cala-diopsis atropurpurea* Madison, Contr. Gray Herb. 208: 97. 1978. TYPE: Ecuador. Los Ríos: Río Palenque Science Center, Km. 56 on Quevedo–Santo Domingo rd., 150–220 m, 3 Aug. 1975, *C. Dodson* 5911 (holotype, SEL!; isotypes, K!, MO!, RPSC not seen, US!). Figure 5A–C.

Terrestrial herb, to 1 m tall; stem erect or decumbent, occasionally with remnants of cataphylls persisting \pm intact at upper nodes; bulbils occurring randomly along its length, usually solitary, 0.5–2 cm long, \pm conical, pointed at apex; sap milky; internodes 0.5–1.5 \times 2–4 cm, weakly glossy, medium green, drying dark brown to greenish brown; cataphylls usually quickly deciduous, (10–)15–30 cm long, acuminate or obtuse with acumen or apiculum at apex (acumen or apiculum 1–1.5 cm long), occasionally inequilateral, acutely or obtusely 1-ribbed abaxially, weakly glossy, dark purple throughout or medium green and entirely or in part irregularly purple-mottled in narrow transverse bands, drying weakly glossy, dark reddish brown. LEAVES 3 to 5, erect-spreading; **petioles** 27–80 cm long, spongy, glabrous, matte, entirely dark purple, or medium green and irregularly dark purple-mottled in narrow transverse bands toward base, drying matte, dark brown or purplish brown to almost black, sheathed 13.5–52 cm, 1/2 to 3/4 of total length; sheath decurrent at apex; free portion 0.5–1 cm diam. midway, terete, subterete, or obtusely D-shaped, weakly and obtusely sulcate at apex; **blades** sagittate or sagittate-subhastate, 25–52 \times 15–33 cm, 1.3 to 2.2 times longer than wide, acute or gradually acuminate to long-acuminate at apex, usually broadest at base, 1 to 1.6 times wider at base than across anterior lobe (measured tip to tip across posterior lobes), weakly or not at all constricted in area of petiole attachment, thin to thinly coriaceous, weakly to moderately bicolorous; upper surface broadly quilted, velvety, dark green, occasionally weakly purple-tinged medially, drying matte to weakly glossy, dark green to brownish green; lower surface weakly glossy to semiglossy, entirely dark purple, or medium green and narrowly to broadly discolorous and dark purple along midrib and major veins, rarely entirely medium green with midrib and major veins dark purple, drying weakly glossy to semiglossy, green to purplish green or discolorous and dark purple-mottled along major veins, rarely purplish brown; anterior lobe 18.8–32.5 \times 15–21 cm,

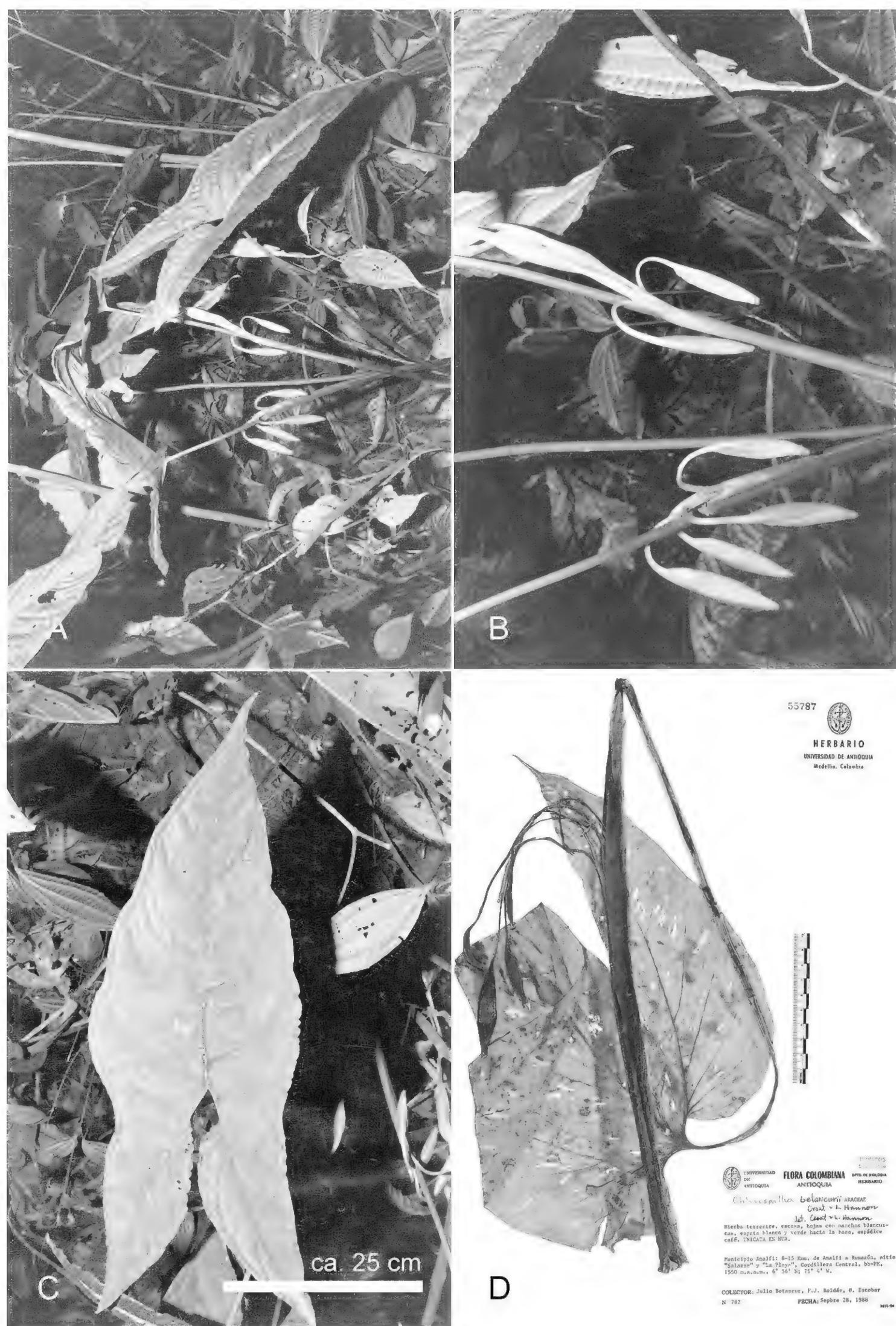


Figure 5. A–C. *Chlorospatha atropurpurea* (Madison) Madison, Croat & Rodríguez 61450. —A. Fertile habit. —B. Close-up of inflorescences. —C. Leaf blade, adaxial surface. —D. *Chlorospatha betancurii* Croat & L. P. Hannon, *Betancur et al.* 782 (HUA holotype).

1.4 to 1.7 times longer than wide, 1.4 to 1.8 times longer than posterior lobes, broadest at or near base, \pm symmetrical; posterior lobes directed toward the base or somewhat outward, $10\text{--}22 \times 4\text{--}10$ cm, 2.1 to 2.2 times longer than wide, acute to bluntly acute or acuminate at apex, occasionally broadly acuminate with the tip narrowly rounded, broadest near base, \pm symmetrical to weakly inequilateral, the inner side occasionally weakly narrower, \pm rounded toward base, briefly to gradually attenuate onto posterior rib; midrib deeply sunken on upper surface, concolorous or occasionally weakly paler than surface, round-raised and purple on lower surface, drying raised, purplish; **basal veins** 3 to 4 pairs, coalesced into prominent posterior rib; posterior rib naked (0.6–) 1.5–3.5 cm per side, occasionally with acute medial rib abaxially; primary lateral veins 5 to 8 pairs, arising at $40^\circ\text{--}65^\circ$, most acutely toward apex, \pm straight, occasionally weakly arcuate, quilted-sunken and concolorous on upper surface, convex to round-raised and purple on lower surface, drying raised, purplish; secondary veins in part obtusely sunken on upper surface, raised on lower surface, drying raised, purplish; tertiary veins raised or prominulous on lower surface, drying entirely or in part raised and otherwise prominulous, darker than surface; reticulate veins obscure; collective veins 3(4), the innermost arising from apex of posterior rib or from uppermost lateral vein on inner side of posterior lobe, loop-connected with all preceding lateral veins, moderately scalloped, 4–9 mm from margin. **INFLORESCENCES** erect, to 6 per axil, producing a strong, fruity fragrance at anthesis; inflorescence cataphyll 1-ribbed abaxially; peduncle held within the sheath, terete to subterete or weakly thicker than broad, $18\text{--}55$ cm \times 1–2 mm, matte, cream to greenish cream or pale yellow, drying tan or occasionally dark brown; **spathe** cucullate, 7.5–12 cm long (1–3 cm longer than spadix), acuminate at apex, obtusely 1-ribbed abaxially, opening \pm broadly $1/2$ to $2/3$ of its length at anthesis and tubular in shape, with blade margins directed forward, drying pale yellow-tan to tan, rarely dark brown; spathe tube weakly glossy to semiglossy, green to cream, rarely weakly purplish on outer surface, semiglossy on inner surface, $3.5\text{--}4.6 \times 0.5\text{--}1.5$ cm, thicker than broad, 3–3.5 cm wide (flattened); spathe blade matte to semiglossy, yellow, yellow-cream, or white on both surfaces, 3.5–3.9 cm long, ca. 1.5 cm wide (flattened), marcescent, erect after anthesis; **spadix** cylindrical, curving weakly forward, stipitate 0.5–1.3 cm, 5–6.3 cm long, adnate to spathe only along stipe or narrowly (to 5 mm) onto pistillate portion at base; stipe and axis pale green; pistillate portion orange (rarely white or magenta),

1.7–2.5 cm \times 3.5–4 mm, usually longer than fertile or sterile staminate portions; fertile staminate portion matte, cream, rarely greenish, $1.3\text{--}2$ cm \times 2.5–3 mm, bluntly acute at apex, cylindrical, occasionally with some synandrodia at and near apex or rarely 1 to 2 purplish staminodes; sterile staminate portion \pm cylindrical, dark purple to purplish white, 1.7–2.2 cm \times 2 mm, weakly narrower than pistillate or fertile staminate portions, frequently longer than fertile staminate portion (rarely the pistillate portion); pistils \pm laxly arranged, 2 to 3(4) across the axis (viewed from above), ca. 2 mm long; ovaries pale green, subglobose or obtusely conical, 1.5–2 mm diam., 2- to 4-locular, with placentation pseudoaxile, the placentae fused toward base and 1-locular at apex, or axile, with placentae fused entire length; ovules 3 to 7 per locule, large, hemianatropous, biseriate; funicle shorter than ovule; style Type 8 (Fig. 1), ca. 1 \times ca. 1.5 mm, comprising slightly more than $1/2$ to $2/3$ of the length of pistil, the margins not coherent with those of adjacent styles; red chromoplasts present; **stigma** white, prominently elevated on and weakly broader at apex than narrowed portion of style, truncate; synandria ca. 1 \times 1.1–1.5 mm, coherent, truncate, rarely weakly concave medially and lobes thickened in some flowers toward apex, (2)3- to 4(5)-lobed, (2)3- to 4(5)-androus; pollen cream-colored, with holes in exine; sterile flowers markedly laxly arranged, ca. 1 \times 1.1–1.5 mm, fungiform, weakly to markedly concave medially, the concave portion dark purple or purplish white, the margins dark purple and sinuate-undulate, rarely entirely cream-colored, in 6 to 7 whorls. **INFRUCTION** 4.5–6.5 cm \times 7–10 mm; berries greenish white, yellow, or pale green, 3.5–4 mm diam.; seeds not known.

Phenology. Flowering occurs in *Chlorospatha atropurpurea* during all months except January and May, with fruiting recorded for the month of July. It is likely that flowering occurs throughout the year. Inflorescences emerge from the petiole sheath in rapid succession, each reaching anthesis no more than one to three days after anthesis of the preceding inflorescence.

Discussion. *Chlorospatha atropurpurea* is widespread on the western slopes of the Andes in Ecuador, having been reported at 100–1200 m elevation in every province except Azuay, Bolívar, Chimborazo, Cotopaxi, Imbabura, and Loja. It would be expected to occur in these provinces, possibly to the south, in Peru, and to the north, into Colombia. The species usually occurs in premontane wet forest but also is found in premontane rainforest and

tropical wet forest. In Cañar, El Oro, and Manabí provinces, it occurs in premontane moist forest. According to *Tipaz et al. 1389*, the local name for this species is chumbil pagande, in Carchi Province.

Chlorospatha atropurpurea is a member of *Chlorospatha* sect. *Occidentales* and characterized by its sagittate, velvety, dark green leaf blades that are occasionally purplish on the upper surface, either dark purple-mottled or entirely dark purple on the lower surface, and by its long, orange style that comprises more than one half to two thirds of the length of the pistil. Also noteworthy is the long sterile staminate portion of the spadix, which comprises approximately one third of the total length, is frequently longer than the fertile staminate portion, and has unusual concave, fungiform flowers. The sterile flowers are laxly arranged, deeply concave (cuplike), sessile or weakly stipitate, and are usually either entirely dark purple or purple with the concave portion white, cream, or purple-tinged. This combination of characters is found in only two other species of *Chlorospatha*, either of which might be confused with *C. atropurpurea* in the sterile state: *C. castula* and *C. hastata*. All three species have leaf blades that are somewhat velvety dark green on the upper surface and either purple-tinged, dark purple-mottled, or entirely dark purple on the lower surface.

Chlorospatha atropurpurea would be most easily confused with *C. castula*, both species having the petiole sheathed one half or more of its length, the sheath decurrent at the apex and the leaf blades sagittate to sagittate-subhastate, with the lobes not markedly constricted at the base, unlike *C. hastata* in which the petiole is sheathed only one third to one half, the sheath free-ending at the apex and the leaf blade hastate, with the lobes moderately to markedly constricted at the base. *Chlorospatha castula* differs from *C. atropurpurea* in having narrower lobes, particularly the posterior lobes, which are 3 to 4 times longer than wide, compared to the relatively broad posterior lobes of *C. atropurpurea*, which are only ca. 2 times longer than wide. Both species have cucullate spathes, but that of *C. castula* is usually shorter, with the tube dark purple. The tube is cream or green in *C. atropurpurea*, with only one report of a green and purplish tinged tube (*Croat 73025*). The spadices of *C. atropurpurea* and *C. hastata* are prominently stipitate and adnate to the spathe only along the stipe or also narrowly onto the pistillate portion, whereas that of *C. castula* is sessile and adnate to the spathe most of the length of the pistillate portion. The stylar morphology found in *C. castula* and *C. hastata* is conspicuously different from that of *C. atropurpurea*, both having Type 4 (Fig. 1)

styles and sessile stigmas, or apparently so. The style of *C. atropurpurea* is Type 8 (Fig. 1) and prominently attenuated, with the mantle thicker than that of the other two species, which have mantles only a few cells thick. In *C. castula*, the style is white, and in *C. hastata*, pink to purplish, very different from the orange style that characterizes *C. atropurpurea*.

The ovaries of *Chlorospatha castula* differ from those of *C. atropurpurea* in having basal placentation, rare in *Chlorospatha*, those of the latter species having axile or pseudoaxile placentation and *C. hastata*, subaxile placentation. *Chlorospatha castula* is known only from Pichincha Province in Ecuador, where it occurs with *C. atropurpurea*, with no collections indicating possible hybridization between the species. The same appears to be true of *C. hastata*, which is sympatric with *C. atropurpurea* in Carchi and Esmeraldas provinces in northern Ecuador. *Jaramillo et al. 5237* (QCA) from Reserva Endesa in Pichincha Province is possibly this species. However, only a Xerox copy was examined. The specimen could not be located at QCA.

Chlorospatha atropurpurea is a strikingly beautiful and colorful plant and has proven to be one of few species that can be maintained in cultivation. Perhaps because it is so wide-ranging, it is somewhat more adaptable than other species. It is one of only a few species known from such a broad area. Of particular note is the wide range of elevation at which the species occurs. However, there appears to be only minor variation in vegetative or floral characters throughout its range.

Additional specimens examined. ECUADOR. **Cañar:** Manta Reál, 620 m, *S. Roponen & A. Johannessen 25:129* (MO). **Carchi:** Tulcán Cantón, Parroquia Tobar Donoso, Sector Sabalera, Res. Indígena, 650–1000 m, *G. Tipaz et al. 1389* (MO, QCNE). **El Oro:** Hac. Daucay, Limón-Playa, 500 m, *X. Cornejo et al. 2442* (GUAY, MO). **Esmeraldas:** Vic. Lita, Lita–San Lorenzo rd., 5 km W of old Río Lita bridge below Lita (prior to 1999), *Croat et al. 82265* (CAS, MO); along Río Bogotá, Awá Community, Río Bogotá, 3 km SW of main Lita–San Lorenzo Hwy., 11.5 km NW of Alto Tambo, 30.5 km W of Río Lita bridge near Lita, *Croat 87557* (K, MO, QCNE); vic. Lita, on Ibarra–San Lorenzo rd., 550–650 m, *Madison et al. 5054* (QCA, SEL); Eloy Alfaro, Reserva Ecol. Cotacachi-Cayapas, Charco Vicente, Río San Miguel at jct. with Río Cayapas, 150 m, *W. Palacios et al. 11289* (MO, QCNE); Eloy Alfaro, Parroquia Luís Vargas Torres, Playa de Oro, Río Santiago, 200 m, *M. Tirado et al. 239* (MO, QCNE). **Guayas:** Cord. Chongón-Colonche, Bosque Protector Loma Alta, 600 m, *X. Cornejo et al. 5219* (GUAY, MO). **Los Ríos:** Río Palenque Science Center, Km. 56 on Quevedo–Santo Domingo rd., 150–220 m, *Dodson 6912* (SEL); Río Palenque Field Station, halfway betw. Quevedo & Santo Domingo de los Colorados, ca. 200 m, *A. Gentry 10130* (MO). **Manabí:** Pedernales Cantón, Res. Ecol. Mache-Chindul, Comun. Ambacha (via coastal edge of Chindul), 250 m, *J. Clark et al. 4174* (MO, QCNE). **Pichincha:** Res. Endesa, Km. 113 on Quito–Puerto Quito

rd., 9 km N of Km. 113, 750 m, *Croat & J. Rodríguez 61450* (K, MO, NY, US); Santo Domingo de los Colorados, vic. La Centinela, 0.2 km past Escuela Mixta La Centinela, 13 km E on trail from main Santo Domingo–Quevedo hwy. in Patricia Pilar, 1000 m, 0°32'S, 79°11'W, *Croat 73025* (MO); forest of the Coop. Santa Marta #2, at Km. 3 of bypass around Santo Domingo de los Colorados, 530 m, *Dodson et al. 8550* (SEL); path along ridge line at La Centinela, at crest of Montañas de Ila, Patricia Pilar–24 de Mayo rd., at Km. 12, 600 m, *Dodson & Benzing 13907A* (SEL), *Dodson & Gentry 12414* (SEL); E side of Río Lelia, ca. 16 km SE of Santo Domingo de los Colorados, *Grayum et al. 9425* (MO); Res. Endesa, Río Silanche, Corp. For. Juan Manuel Durini, Km. 113 on Quito–Puerto Quito hwy., 10 km N of main hwy., 650–700 m, *Jaramillo 6788* (MO, QCA), *Jaramillo 7020* (COL, QCA).

Cultivated specimens examined. ECUADOR. **Esmeraldas:** Vic. Lita, Lita–San Lorenzo rd., *Croat 81258* (MO); vic. Lita, 6.4 km W of old Río Lita bridge (prior to 1999), at Río Piguambí, 685 m, *L. P. Hannon 97-052* (MO), *L. P. Hannon 97-340* (MO). **Los Ríos:** Río Palenque Science Center, 1977, *Madison 4187* (SEL), from type clone, *Dodson 5911*.

4. *Chlorospatha bayae* Croat & L. P. Hannon, sp. nov. TYPE: Colombia. Valle: along old Calí–Buenaventura rd., 50.5 km N of Agua Clara, 31.2 km S of jct. with main Calí–Buenaventura Hwy., ca. 1100–1200 m, 3°31'N, 76°45'W, 6 July 1993, *Croat & D. Bay 75600* (holotype, MO-04570991-92!; isotype, CUVCI). Figures 6D, 7A–C.

Herba usque ad 1 m; internodia 1–3 cm longa, usque ad 3 cm lata; cataphylla 10–21 cm longa. Petiolus 62–72 cm longus, vaginatus per 37–41 cm; lamina foliaris sagittata, 24.5–35 × 11.5–19 cm, lobis posterioribus 8–12 × 4.8–8 cm, nervis basalibus utroque 6 vel 7, nervis primariis lateralibus utroque 8 ad 10. Inflorescentiae erectae, 2 ad 4 in quaque axilla; pedunculus 30–41 cm × ca. 2 mm; spatha 12.5–14.5 cm longa, 5–7 mm diam., lamina alba, 6–7 cm × 6–8 mm; spadix 10.7–12 cm longus, sessilis.

Terrestrial herb, to ca. 1 m tall; stem with remnants of old cataphylls persisting intact at uppermost nodes, otherwise fibrous with fragments of epidermis at remaining nodes, the fibers pale; internodes 1–3 × to 3 cm, dark green to gray, drying weakly glossy, tan (all measurements made from dried material); cataphylls quickly collapsing, 10–21 cm long, apex not known, drying weakly glossy to semiglossy, medium-dark to dark brown. LEAVES 2, erect-spreading; **petioles** 62–70 cm long, moderately firm, glabrous, medium yellow-green, drying weakly glossy, medium-dark to dark reddish brown, sheathed 37–41 cm, more than 1/2 of total length (less than 2/3); sheath decurrent at apex; free portion 4–6 mm diam. midway, terete; **blades** sagittate, 24.5–35 × 11.5–19 cm, 1.8 to 2.1 times longer than wide, acuminate at apex, broadest at base, 1.1 to 1.2 times wider at base than across anterior lobe (measured tip

to tip across posterior lobes), subcoriaceous, moderately bicolorous, weakly or not at all constricted in area of petiole attachment, drying subcoriaceous; upper surface ± flat (not quilted), semiglossy, dark green, drying matte to weakly glossy, dark olive-green; lower surface semiglossy, drying matte to weakly glossy, occasionally in part semiglossy, greenish yellow-brown; anterior lobe 18–26 × 10.3–16 cm, 1.6 to 1.7 times longer than wide, 2.2 to 2.3 times longer than posterior lobes, broadest below middle, ± symmetrical; posterior lobes directed toward base, 8–12 × 4.8–8 cm, 1.5 to 1.7 times longer than wide, narrowly rounded or bluntly acute at apex, broadest at base, weakly to moderately inequilateral, the inner side narrower, ± rounded toward base, decurrent onto petiole (possibly terminating at petiole apex); outer side 1.1 to 2 times wider than inner side midway, ± straight toward base, occasionally weakly concave; major and secondary venation drying ± wrinkled on lower surface; midrib sunken on upper surface and concolorous, convex on lower surface, paler than surface, drying raised, weakly paler to weakly darker than surface; **basal veins** 6 to 7 pairs, coalesced into prominent posterior rib; primary lateral veins 8 to 10 pairs, arising at 55°–70°, weakly to moderately arcuate, narrowly sunken on upper surface, convex on lower surface, drying raised, weakly paler to weakly darker than surface; secondary veins in part obtusely sunken on upper surface, raised on lower surface, drying raised, ± concolorous; tertiary veins darker than lower surface, drying prominulous, ± concolorous; reticulate veins drying obscure; collective veins 3, the innermost arising from one of the lowermost lateral veins on the inner side of the posterior lobe, loop-connected with all preceding lateral veins, ± parallel to and 2–6 mm from margin. INFLORESCENCES erect, 2 to 4 per axil; peduncle held within the sheath, 30–41 cm × ca. 2 mm, drying weakly glossy, medium-dark reddish brown; **spathe** weakly cucullate, 12.5–14.5 cm long, ± acute at apex, obtusely ribbed abaxially; spathe tube green along rib on outer surface, otherwise dark purple on both surfaces, 6.2–7.5 cm × 5–7 mm, drying matte to weakly glossy, dark blackish brown on outer surface, weakly to moderately paler on inner surface; spathe blade white, 6–7 cm × 6–8 mm, drying matte to weakly glossy, brownish cream to medium-dark tan on both surfaces, marcescent, erect after anthesis; **spadix** erect, 10.7–12 cm long, sessile, adnate to spathe 5–6 cm at base, the entire length of pistillate portion; pistillate portion creamy white, 5–6 cm × ca. 2.5 mm, drying medium-dark reddish brown; fertile staminate portion pale yellow-brown, 3.5–4.2 cm × 2–4 mm, bluntly acute



Figure 6. A–C. *Chlorospatha besseae* Madison. A, B photographed from MO cultivar, *Croat & L. P. Hannon 81474* (= *Hannon 97-386*). —A. Fertile habit. —B. Plant with inflorescence at anthesis. —C. Close-up of inflorescences (one cut open to expose pistillate portion of spadix), *Croat et al. 82131* (MO). —D. *Chlorospatha bayae* *Croat & L. P. Hannon, Croat & Bay 75600* (MO holotype, sheet 1 of 2).



Figure 7. A–C. *Chlorospatha bayae* Croat & L. P. Hannon from the original collection and holotype. —A. Leaf blade adaxial surfaces. —B. Fertile habit. —C. Close-up of petioles and inflorescences. —D. *Chlorospatha bogneri* Croat & L. P. Hannon, Croat 69556 (MO paratype).

at apex, ellipsoid, drying medium-dark reddish brown; sterile staminate portion 1.2–1.6 cm \times 2–3 mm, broadest at apex, drying dark blackish brown; pistils \pm laxly arranged, 1 to 3 across the axis (viewed from above), 1.5–2 mm long; ovaries subglobose, ca. 1 \times 1.8–2.2 mm, drying medium brown with darker veins; style Type 9 (Fig. 1), 0.5–0.8 \times 1.5–2 mm, the margins not coherent with those of adjacent styles; **stigma** golden tan, ca. 0.3 mm diam., elevated on and weakly broader than narrowed portion of style, drying dark reddish brown; synandria ca. 1 \times 1.5–2 mm, occasionally \pm elongated in direction of axis, coherent, truncate to obtusely truncate, 3- to 4(5)-lobed, 3- to 4(5)-androus (mostly 4); sterile flowers 0.8–1 \times 0.5–2 mm, elongated in direction of axis, laxly arranged in 7 whorls (axis naked between whorls), 1- to 6-branched, the branches \pm clavate. INFRUCTESCENCE 9.5 cm \times 8 mm, drying weakly glossy to semiglossy, dark reddish brown on outer surface, semiglossy and moderately paler on inner surface; berries 3–4.5 \times 2–5 mm, drying dark tan.

Phenology. Flowering is only known to occur in *Chlorospatha bayae* during the month of July.

Etymology. *Chlorospatha bayae* is named for Dorothy Bay (Missouri Southern College), one of the collectors of the type and an expert on the Flora of Bajo Calima in Valle Department of Colombia.

Discussion. *Chlorospatha bayae* is known only from the type collection from the western slopes of the Cordillera Occidental, in premontane wet forest or possibly premontane moist forest. The species is a member of *Chlorospatha* sect. *Occidentales* and distinguished by its sagittate, subcoriaceous, semiglossy, dark green leaf blades, medium green petioles, and large inflorescence (12.5–14.5 cm long), with most of the spathe tube dark purple on both surfaces. The blades have numerous primary lateral veins (eight to 10 pairs) and dry unusually thick, with the major and secondary venation prominently wrinkled on the lower surface.

Chlorospatha bayae could possibly be confused with *C. jaramilloi* and *C. sagittata*, known only from the western slopes of the Andes in Ecuador, in Pichincha and Imbabura provinces, respectively, the leaf blades being similar in shape and drying color and the spathe tubes purple or purplish. In the latter two species, the leaf blades dry thin, the lower surface more or less glossy, and the major venation flattened and smooth (not wrinkled), differing from those of *C. bayae*, which are subcoriaceous and dry unusually thick, mainly matte to weakly glossy on the

lower surface, with the major and secondary venation prominently raised and conspicuously wrinkled. The velvety living blades of *C. sagittata* further differ from the semiglossy blades of *C. bayae*, which have eight to 10 pairs of primary lateral veins versus six or seven pairs in *C. jaramilloi* and *C. sagittata*. The petiole in *C. bayae* and *C. jaramilloi* is sheathed one half of its length, with the sheath decurrent at the apex, differing from that of *C. sagittata*, which is sheathed more than three fourths of its length, with the sheath free-ending. The inflorescence of *C. bayae* is larger than those of the other two species (12.5–14.5 cm long vs. less than 12 cm long). The peduncles of *C. sagittata* are significantly longer than those found in either *C. bayae* or *C. jaramilloi*, 88 cm long and more than three fourths as long as the petiole versus one half as long as the petiole in the other two species, with the peduncle 30–41 cm long in *C. bayae* and only 18–20 cm long in *C. jaramilloi*. The spadix in *C. bayae* and *C. jaramilloi* is adnate to the spathe the entire length of the pistillate portion versus one half of the length in *C. sagittata*. In *C. bayae*, the pistillate portion of the spadix is significantly longer than the fertile staminate portion (ca. 2 cm longer), whereas in the other two species, it is shorter than that portion. The style is long-attenuated in *C. jaramilloi* (Type 5, Fig. 1), comprising one half of the length of the pistil, and briefly attenuated in *C. bayae* (Type 9, Fig. 1), comprising one third of the length of the pistil. The style is significantly different in *C. sagittata* (Type 4, Fig. 1), comprising less than one fourth of the length of the pistil, with the stigma apparently sessile. The synandria of *C. sagittata* are 4- to 6-androus versus 3- to 4-androus in the other two species. The sterile flowers are branched in both *C. bayae* and *C. jaramilloi*, but are densely arranged in the latter species and laxly arranged in *C. bayae*. These are subprismatic and laxly arranged in *C. sagittata*.

Chlorospatha bayae could not be easily confused with any species, but it could possibly be confused with *C. yatacuensis*, which occurs in the same general area, but with *C. bayae* occurring at higher elevations along the old Calí–Buenaventura road, 50.5 km north of Agua Clara, on the western slopes of the Cordillera Occidental in Valle Department, Colombia, at 1100–1200 m elevation. Both species are similar in size, with leaf blades of similar shape; however, the blades of *C. bayae* have eight to 10 pairs of primary lateral veins and dry subcoriaceous, with the major and secondary venation prominently raised and wrinkled. The blades of *C. yatacuensis* have four pairs of primary lateral veins and dry thin, with only the midrib and secondary veins weakly raised and none of the venation wrinkled. The petiole of *C. bayae* is

sheathed more than one half of its length and the peduncle is long (30–41 cm long), as is the inflorescence (12.5–14.5 cm long) in which the spathe tube is dark purple on both surfaces. *Chlorospatha yatacuensis* differs in having the petiole sheathed one third of its length, the peduncle less than 22 cm long, the inflorescence markedly small (4.2–5.5 cm long), and the spathe entirely cream-colored. The spadix of the latter species is adnate to the spathe one half of the length of the pistillate portion and the sterile flowers are prismatic. The spadix of *C. bayae* is adnate the entire length of the pistillate portion and the sterile flowers are 1- to 6-branched.

5. *Chlorospatha besseae* Madison, Selbyana 5(3–4): 352. 1981. TYPE: Ecuador. Esmeraldas: environs of Lita, on Ibarra–San Lorenzo RR, 550–650 m, 10 June 1978, *M. Madison, T. Plowman, H. Kennedy & L. Besse 5144* (holotype, SEL!; isotypes, F!, K!, MO!, QCA!). Figure 6A–C.

Terrestrial herb, to 80 cm tall, in small colonies; stems decumbent, to 50 cm long, erect to 30 cm, occasionally with remnants of old leaf bases and cataphylls persisting \pm intact at upper nodes; internodes 1–4 \times 1.3–3 cm, weakly glossy to semiglossy, pale, medium or dark green (rarely purplish), becoming grayish green or brown with age, drying matte, dark reddish brown; cataphylls 7–11 cm long, apex not known, pale to medium green, drying matte, dark brown. LEAVES 2 to 5, erect-spreading; **petioles** 17–33.5 cm long, moderately firm, glabrous, matte, medium to dark green, drying matte to weakly glossy, medium-dark to dark reddish brown, sheathed 10–18 cm, ca. 1/2 to slightly more than 2/3 of total length; sheath decurrent at apex; free portion 2–4 mm diam. midway, terete, entirely weakly and narrowly sulcate or in part sharply V-sulcate toward apex and otherwise smooth; **blades** held \pm horizontally to erect-spreading, ovate-sagittate, cordate at base, 12.5–23(–28) \times 7–14(–16) cm, 1.5 to 1.8(to 2.1) times longer than wide, weakly to moderately or occasionally abruptly acuminate at apex, broadest across anterior lobe, 1.4 to 1.9 times wider across anterior lobe than at base (measured tip to tip across posterior lobes), thin, conspicuously bicolorous; upper surface \pm quilted, matte-subvelvety or velvety, dark to medium green, drying weakly glossy, dark green to olive-green or blackish brown; lower surface reticulate, narrowly matte and minutely colliculate along all orders of venation, otherwise semiglossy, drying weakly glossy to semiglossy, moderately to prominently paler; anterior lobe 10–18 \times 7–14(–16) cm, 1.1 to 1.4 times longer than

wide, 2.3 to 3.3 times longer than posterior lobes, broadest at or below middle, \pm symmetrical to weakly inequilateral, with one side to 1 cm wider than opposite side; posterior lobes directed toward the base, (2–)3–7.5 \times 2.8–5.6 cm, 1 to 1.2(to 1.4) times longer than wide, narrowly rounded to bluntly rounded at apex, broadest at base, moderately to markedly inequilateral, the inner side narrower, \pm rounded toward base, briefly attenuate and decurrent onto petiole; outer side 1.7 to 5 times wider than inner side midway, \pm convex to weakly constricted toward base; all orders of venation matte on lower surface; midrib narrowly sunken on upper surface, concolorous to weakly paler than surface, round-raised on lower surface, drying raised, moderately darker than surface; **basal veins** 3 to 4 pairs, coalesced into a prominent posterior rib; primary lateral veins 4 to 5(6) pairs, arising at 30°–65°, most acutely toward apex, weakly to moderately arcuate, narrowly sunken on upper surface, concolorous to occasionally in part weakly paler than surface toward the base, round-raised or narrowly raised on lower surface, drying raised to weakly flattened, moderately darker than surface; secondary veins in part obtusely sunken on upper surface, raised on lower surface, drying weakly raised, concolorous to weakly darker than surface; tertiary veins prominulous on lower surface, drying in part weakly prominulous, otherwise visible and distinct, concolorous to weakly darker than surface; reticulate veins prominulous on lower surface, drying visible, distinct, flat, concolorous to weakly darker than surface; collective veins 3, the innermost arising from one of the lateral veins on inner side of posterior lobe, rarely from apex of posterior rib, loop-connected with all preceding lateral veins, weakly scalloped, 3–8 mm from margin. INFLORESCENCES erect, 1 to 3 per axil, emitting a sweet fragrance at anthesis; peduncle held within the sheath, 10–19.5 cm \times 1–4 mm, obtusely D-shaped in apical 1/2, wider than thick toward apex (to 4 mm wide), narrowing toward base, matte, pale green, drying matte to weakly glossy, dark brown or greenish brown to dark green; **spathe** erect, 5–7 cm long, ovate-elliptic, cuspidate at apex, obtusely 1-ribbed abaxially in apical 1 cm; spathe tube semiglossy, pale green to yellow-green cream on outer surface, glossy on inner surface, 2.2–3.5 cm \times 4–7 mm, drying matte to weakly glossy, medium to dark brown, weakly paler on inner surface; spathe blade matte, cream or yellow-green cream, weakly paler than tube on both surfaces, 2.3–4 cm \times 5–9 mm, opening broadly at anthesis and broadly funnel-shaped, the margins directed \pm outward, drying matte to weakly glossy on outer surface, weakly paler on inner surface,

marcescent, erect after anthesis; **spadix** erect, held weakly forward at anthesis, (3.5–)4–5.8 cm long, sessile, adnate to spathe 1.5–2.3 cm at base, most or all of the length of pistillate portion; pistillate portion rose-colored (rarely cream), 2–2.5 cm \times ca. 4 mm, wider than thick, weakly broadest midway, drying dark reddish brown; fertile staminate portion matte, bright orange, turning deep red when cut, 2.1–2.6 cm \times ca. 4 mm, \pm cylindrical to weakly tapering, narrowly rounded at apex, drying orange to dark orangish brown; sterile staminate portion cream to yellowish cream toward base, pale to medium yellow-orange at apex, 3.4–4 \times 3–4 mm, \pm cylindrical, drying medium orange at apex, weakly lavender-tinged gray toward base; pistils weakly coherent, 3 to 4 across the axis (viewed from above), 1.3–1.7 mm long; ovaries \pm cylindrical, cream to greenish cream or creamy white (drying whitish), 0.8–1.2 \times ca. 1.5 mm, 2-locular, with axile or subaxile placentation; ovules 6 to 10 per locule, hemianatropous, biseriate; funicle as long as ovule; style Type 9 (Fig. 1), rose-colored, densely darker rose-speckled, 0.5–0.7 \times ca. 1.5 mm, the margins weakly coherent with those of adjacent styles; **stigma** whitish, ca. 0.5 mm diam., disklike, weakly elevated on style; synandria 1–1.5 \times 1.5–2 mm, coherent, truncate, 3- to 5-lobed, 3- to 5-androus (mostly 4); sterile flowers 0.5–1 mm long, 1–1.3 \times 1 mm diam. and weakly elongated in direction of axis, coherent, truncate, irregularly subprismatic to prismatic, in 2 to 4 whorls. **INFRACTESCENCE** drying 5.6 cm \times 6 mm, matte, dark brown; berries white, drying 2.5–3.5 mm diam., pale tan.

Phenology. Flowering is reported in *Chlorospatha besseae* for the months of June, October, November, and December. In cultivation, the species flowers periodically throughout the year but not continuously. Inflorescences emerge in slow progression, with several days between anthesis of one inflorescence and emergence of the next inflorescence at the apex of the petiole sheath. Fruiting is recorded only for the month of December.

Discussion. *Chlorospatha besseae* is known only from premontane wet forest and lower montane wet forest on the western slopes of the Andes in Carchi and Esmeraldas provinces in northwestern Ecuador at 550–814 m elevation and would be expected to occur to the north, along the border in southern Colombia. The species is a member of *Chlorospatha* sect. *Occidentales* and occurs in small colonies, the latter a condition that distinguishes it from most species of *Chlorospatha*, particularly those from the western slopes. The species is also distinguished by its velvety, ovate-sagittate leaf blades that are cordate

at the base, with the posterior lobes short and rounded at the apex, and its small inflorescence with bright orange synandria and rose-colored styles. It is one of only three species from the western slopes or Magdalena River drainage that have the leaf blade narrowly, minutely colliculate along all abaxial venation. This condition is also easily observed in dried material and is rarely encountered in species from the western slopes.

Chlorospatha besseae would be most easily confused with *C. bogneri* from La Planada Reserve in Nariño Department in southern Colombia, at 1700–2050 m elevation. The leaf blades of *C. bogneri* are subcordate to nearly truncate at the base, with the posterior lobes usually acute to bluntly acute at the apex and only occasionally narrowly rounded. The upper surface of the blade of *C. bogneri* is minutely rugose and all orders of venation are prominently raised, granular-puberulent to minutely puberulent on the lower surface and darker than the surface. The lower surface in *C. bogneri* lacks the characteristic colliculate border that occurs along the veins in *C. besseae*. *Chlorospatha bogneri* differs in having the petiole entirely or partially minutely many-ribbed, frequently entirely or partially minutely puberulent to granular-puberulent and occasionally purple-tinged. The most obvious difference lies in its sheathing, which, unlike that of *C. besseae*, is three fourths as long to nearly as long as the petiole, with the sheath prominently free-ending at the apex, such extensive sheathing being uncommon in *Chlorospatha*. As would be expected, the peduncles of *C. bogneri* are proportionally much longer than those of *C. besseae*, being equal in length to or longer than the petioles.

The inflorescences of *Chlorospatha besseae* and *C. bogneri* are small and the synandria bright orange, but the spadix of the latter species is weakly stipitate and adnate to the spathe one half of the length of the pistillate portion. In both species, the style is Type 9 (Fig. 1), but is deeply rose-colored in *C. besseae* and green in *C. bogneri*, in which this portion of the spadix is more than twice as long, with the sterile flowers more laxly arranged in six whorls. The two species are possibly closely related. Only five species have bright orange synandria and all occur in the frontier region along the border between Colombia and Ecuador, on the western slopes of the Andes: *C. besseae*, *C. bogneri*, *C. dodsonii*, *C. litensis*, and *C. mansellii*. Only *C. dodsonii* is widespread (in Ecuador).

Chlorospatha besseae might be confused with *C. mansellii*. The species are sympatric in the Lita–San Lorenzo region of Esmeraldas Province, Ecuador. *Chlorospatha mansellii* is a somewhat larger plant

with hastate-drying blades, with the posterior lobes acute at the apex and both longer and narrower (ca. 2 times longer than wide and two thirds as long as the anterior lobe) than those of *C. besseae*. The inflorescences are similar, but that of *C. mansellii* is consistently and significantly larger, with the fertile staminate portion tapering, acute to bluntly acute at the apex and longer than the pistillate portion. Both species have Type 9 styles (Fig. 1), but those of *C. mansellii* are pink-tinged orange. It is possible that *C. mansellii* is a hybrid taxon with *C. besseae* as one of the hybrid parents.

Chlorospatha besseae could be confused with *Chlorospatha* sp. indet. 1 from Nariño Department in southern Colombia. No fertile material of this species was examined, but the label notes report the spathe tube as medium green and dark purple at the apex. The species have similar blade shapes and petiole sheathing. *Chlorospatha* sp. indet. 1 either terminates at the petiole apex or is possibly weakly confluent with that of the opposite lobe. The major veins on the lower surface of the blade dry flattened in *Chlorospatha* sp. indet. 1 but raised in *C. besseae*. *Chlorospatha* sp. indet. 1 has only three pairs (rarely four) of primary lateral veins. The petiole of Species 1 is soft, semiglossy, and green with darker transverse markings and dries weakly glossy, with the epidermis partially separated intact from the petiole.

Additional specimens examined. ECUADOR. **Carchi:** El Pailón, 45 km below Maldonado, along footpath to Tobar Donoso, *Madison & Besse* 7072 (SEL), 7279 (K, QCA, SEL, US). **Esmeraldas:** Lita–San Lorenzo rd., 3.7 km W of old Río Lita bridge below Lita (prior to 1999), 647 m, *Croat et al.* 82131 (HUA, K, MO, QCA, QCNE, UB, US); Lita–San Lorenzo rd., 13 km W of Río Lita bridge (new rd., after 1998), 814 m, *Croat et al.* 83223 (MO, QCNE, USM).

Cultivated specimens examined. ECUADOR. **Esmeraldas:** Lita–San Lorenzo rd., 3.4 km W of old Río Lita bridge below Lita (prior to 1999), *Croat & L. P. Hannon* 81474 (MO, cult. from *L. P. Hannon* 97-386); vic. Lita, 600 m, *Madison* 6740 (SEL, cultivated from type *Madison et al.* 5144; Selby live acc. 78-1086).

6. *Chlorospatha betancurii* Croat & L. P. Hannon, *Aroideana* 27: 9–11. 2004. TYPE: Colombia. Antioquia: Cordillera Central, Mpio. Amalfi, 8–15 km from Amalfi on Amalfi–Rumazón rd., sites Salazar & La Playa, 1550 m, 06°56'N, 75°04'W, 28 Sep. 1988, *J. Betancur, F. Roldán & O. Escobar* 782 (holotype, HUA!). Figure 5D.

Terrestrial herb, ca. 1 m tall; stem with remnants of old cataphylls persisting in part as short fibers at upper nodes, the fibers pale to dark brown (all measurements made from dried material); internodes (of juvenile plants) 9–10 × 8–11 mm, drying weakly

glossy, dark greenish brown; cataphylls ca. 37 cm long, acuminate at apex, drying semiglossy, medium tan or brown. LEAVES 1; **petiole** 77 cm long, drying glabrous, weakly glossy to semiglossy, dark reddish brown, with epidermis much paler, in part separated ± intact and semi-transparent, sheathed ca. 38 cm, ca. 1/2 of total length; sheath decurrent at apex; free portion 5–7 mm diam. midway; **blade** deeply 3-lobed, 30 × 29 cm, about as long as wide, drying thin, weakly bicolorous; upper surface green, sparsely, irregularly whitish maculate, drying weakly glossy, dark green, the maculations pale-medium green; lower surface drying semiglossy to glossy, the maculations pale yellow-green; **medial lobe** 28 × 10 cm, 2.7 times longer than wide, acuminate at apex, broadest below middle, weakly shorter than to weakly longer than lateral lobes, briefly attenuate toward base, broadly attached, ca. 3.5 cm wide at point of attachment, weakly inequilateral; **lateral lobes** directed toward the apex, 26.5–28.5 × 8–8.5 cm, 3.4 to 3.6 times longer than wide, gradually acuminate to long-acuminate at apex, broadest near base, markedly inequilateral, the inner side always narrower, long attenuate toward base and moderately confluent with medial lobe, the confluent portion ca. 1.5 cm wide; outer side ca. 2.2 times wider than inner side midway, ± rounded or oblique at base; midrib round-raised on lower surface, drying ± flattened, darker than surface; posterior rib naked 1.3–1.5 cm per side; primary lateral veins (of medial lobe) 6 pairs, arising at 30°–45°, straight to weakly arcuate, round-raised on lower surface, drying raised at base, otherwise ± flattened, darker than surface; primary lateral veins (of lateral lobes) 7 to 8 pairs, the basal pair briefly fused toward base, straight to weakly arcuate; secondary veins drying weakly raised on lower surface, weakly darker than surface; tertiary veins drying in part weakly prominulous, otherwise flat, mostly concolorous on lower surface, in part weakly darker than surface; reticulate veins drying obscure; collective veins 3, the innermost arising from lowermost lateral vein at base, loop-connected with all preceding lateral veins, moderately scalloped, 3–10 mm from margin. INFLORESCENCES erect, to 5 per axil; peduncle held within the sheath, 37–44 cm × ca. 2 mm, drying matte to weakly glossy, dark brown; **spathe** erect, total length not known; spathe tube green, 2.5–3 cm × 3.5 mm, drying matte to weakly glossy, dark reddish brown on outer surface, weakly glossy on inner surface and densely pale tan, punctiform (speckles regularly rounded, appearing as subepidermal cellular inclusions); spathe blade white, length not known; **spadix** erect, 6 cm long, sessile, adnate to spathe ca. 1 cm at base,

ca. 1/2 of the length of pistillate portion; pistillate portion ca. 2.2 cm \times ca. 2 mm, drying brown; fertile staminate portion brown, ca. 2.8 cm \times 1.5–3 mm, clavate, bluntly rounded at apex, drying dark reddish brown; sterile staminate portion ca. 1 cm \times 1–1.5 mm, broadest at base, drying medium yellow-brown; pistils weakly coherent (laxly arranged in basal whorls), 2 to 4 across the axis (viewed from above), ca. 1 mm long; ovaries subglobose, ca. 0.8 \times 1–1.5 mm, drying medium brown; style Type 3 (Fig. 1), 0.8–1 mm diam., the margins not coherent with those of adjacent styles; **stigma** 0.2–0.3 mm diam., sessile; synandria ca. 1 \times ca. 1 mm, coherent, truncate, deeply (2)3- to 4-lobed, 3- to 4-androus (mostly 3); sterile flowers ca. 0.5 mm long, 1.7–2 \times 1 mm diam. and \pm elongated in direction of axis, \pm coherent, truncate, irregularly subprismatic, in 6 whorls. **INFRACTESCENCE** 4–6.3 \times 0.9–1.4 cm, drying matte to weakly glossy, dark reddish brown; berries 3–4 mm diam., drying dark brown; seeds not known.

Phenology. Flowering and fruiting are only known to occur in *Chlorospatha betancurii* during the month of September.

Discussion. *Chlorospatha betancurii* is known only from tropical wet forest on the eastern slopes of the Cordillera Central in Antioquia Department, Colombia, at 1550–1850 m elevation, a region of significant endemism in *Chlorospatha*. The species is a member of *Chlorospatha* sect. *Chlorospatha* and is distinguished by its deeply 3-lobed, whitish maculate, green leaf blades that dry green on both surfaces, with the lateral lobes long-acuminate at the apex, narrower than and nearly as long as the medial lobe. The petiole dries semiglossy, with the epidermis partially separated intact from the main body and semi-transparent. The spadix is relatively small (6 cm long), with the fertile staminate portion brown.

Chlorospatha betancurii is one of only three trilobed species that occur in the region east of the Cordillera Occidental, and it could be confused with only one of these, *C. callejasii*, also from Antioquia Department, near Yarumal. The leaf blades of the latter species are not maculate and dry rich, reddish brown on both surfaces, with the upper surface matte-subvelvety and the major and secondary venation almost black on the lower surface. All segments are acute at the apex, with nine to 11 pairs of primary lateral veins on the lateral segments. The blades of *C. betancurii* are maculate and dry green on both surfaces, weakly glossy on the upper surface, with the abaxial venation only moderately darker than the surface, all segments long-acuminate at the apex and

seven or eight of the primary lateral veins on the lateral segments. The fertile staminate spadix of *C. callejasii* is white, whereas that of *C. betancurii* is brown.

Chlorospatha betancurii might also be confused with *C. cogolloi*, but the latter species occurs only on the western slopes of the Cordillera Occidental. *Chlorospatha cogolloi* differs in usually having the petiole sheathed three fourths or more of its length, with the epidermis not separating (on drying); the petiole is sheathed about half of its length in *C. betancurii*, with the epidermis partially separated (on drying), semi-transparent, and semiglossy. The blades of *C. cogolloi* are usually entirely purple on the lower surface, rarely green with the major veins purple; in *C. betancurii*, the lower blade surface is green. In *C. cogolloi*, there are more pairs of primary lateral veins on all segments (in mature specimens), with 10 pairs on the medial lobe, eight to 10 pairs on the lateral lobes versus six pairs on the medial lobe, and seven or eight pairs on the lateral lobes in *C. betancurii*. The spadix of *C. cogolloi* is also longer than that of *C. betancurii*, in specimens of comparable size, with the fertile staminate portion white, whereas that of *C. betancurii* is brown.

Chlorospatha betancurii bears a superficial resemblance to *C. mirabilis*, both having deeply 3-lobed blades; however, the latter species occurs only on the western slopes of the Cordillera Occidental and in Panama, and the lower surface of the blade is entirely purple or purplish, thus differing from that of *C. betancurii*, which is green. The sterile staminate portion of the spadix comprises only one fifth of the total length in the latter species, with the sterile flowers densely arranged, and one third of the total length in *C. mirabilis*, with the sterile flowers laxly arranged.

The second collection cited, *L. Escobar et al.* 7961, is a very small, sterile specimen from the same general area as the type and, therefore, is included here.

Additional specimen examined. COLOMBIA. **Antioquia:** Mpio. Gautapé, Santa Rosa trail, Finca Montepinar, *L. Escobar et al.* 7961 (paratype, MO).

7. *Chlorospatha bogneri* Croat & L. P. Hannon, *Aroideana* 33: 78–81. 2010. TYPE: Colombia. Nariño: La Planada Reserve, on trails La Vieja and La Piña, NW of Science Center, 1850–2050 m, 1°09'40"N, 77°58'78"W, 8 June 1996, *J. Bittner* 2493 (holotype, MO-05053495!; isotype, PSO!). Figures 7D, 8A, B.

Terrestrial herb, to 1.2 m tall (all measurements made from dried material); stem decumbent, to 34 cm

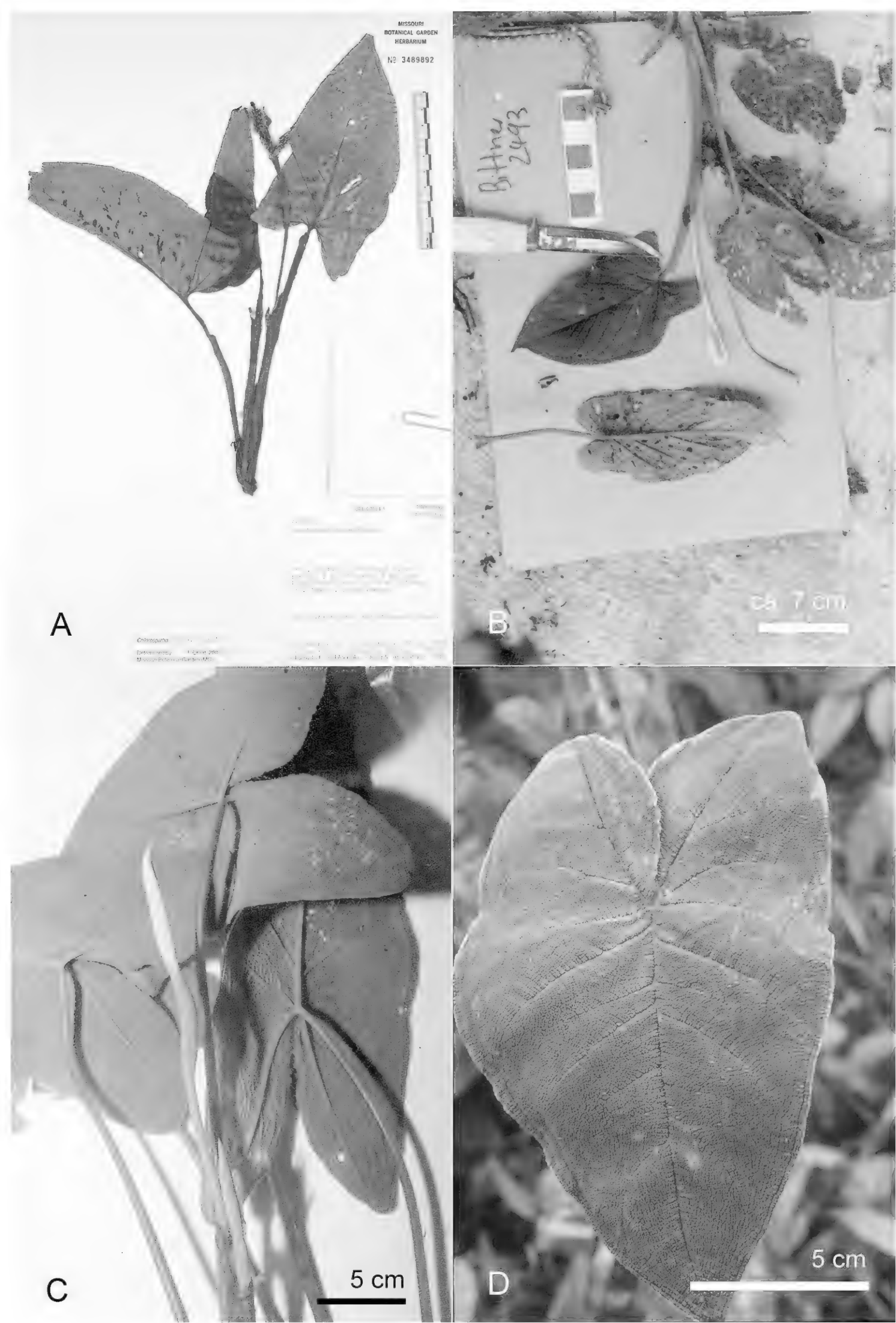


Figure 8. A, B. *Chlorospatha bogneri* Croat & L. P. Hannon. —A. *Gentry et al.* 55072 (MO paratype). —B. Live type collection on ground, *Bittner* 2493. —C. *Chlorospatha* sp. indet. 3, flowering plant, pre-anthesis, *Croat & Gaskin* 79662 (MO). —D. *Chlorospatha bullata* Croat & L. P. Hannon, leaf blade adaxial surface, *Croat* 50130 (MO).

long; sap milky; internodes 1.5–3 cm \times 3–9 mm, weakly glossy, dark green, occasionally violet-tinged, drying matte, dark brown to blackish brown; cataphylls quickly deciduous, 6–16 cm long, obtuse with acumen at apex, dark green, drying matte, dark brown to blackish brown. LEAVES 2 to 7, erect-spreading; **petioles** 10–23 cm long, frequently minutely many-ribbed near apex, rarely entirely \pm minutely crispy-puberulent or in part only near apex and otherwise granular-puberulent or minutely puberulent, matte, dark green, occasionally violet-tinged, drying matte, dark blackish brown, sheathed 8–22.5 cm, more than 3/4 of to almost entire length; sheath free-ending at apex, frequently prominently so, the margins in-rolled; free portion 2–3.5 mm diam. midway, terete, sharply V-sulcate; **blades** erect-spreading, ovate or narrowly ovate-sagittate, subcordate or subtruncate at base, 10–18 \times 5–9.2 cm, 4.5–7.3 cm wide at base, (1.3 to)1.7 to 2.2 times longer than wide, weakly to moderately acuminate at apex, usually weakly broader across anterior lobe than at base, 1 to 1.4 times wider (measured tip to tip across posterior lobes), occasionally with one or both margins weakly to moderately constricted in area of petiole attachment, moderately thin, moderately to prominently bicolorous; upper surface minutely rugose, matte, markedly dark green, drying matte, dark blackish brown, rarely weakly greenish; lower surface reticulate, matte, drying weakly glossy, occasionally semiglossy, weakly to moderately paler; anterior lobe 9–16 \times 4.5–9.2 cm, 1.6 to 1.8(to 3.5) times longer than wide, (3.3 to)3.6 to 4 times longer than posterior lobes, broadest at or below middle, \pm symmetrical to weakly inequilateral; posterior lobes directed toward the base, 2.5–4.5 \times 2.5–3.8 cm, 1 to 1.2 times longer than wide, usually as wide as long, acute to bluntly acute at apex, occasionally narrowly rounded, broadest at base, markedly inequilateral, the inner side narrower, weakly rounded to acute toward base, briefly attenuate and decurrent onto petiole; outer side (2.1 to)3.2 to 4.4 times wider than inner side midway; all orders of venation narrowly sunken on upper surface, prominently raised on lower surface, granular-puberulent to minutely puberulent, rarely crispy-puberulent, darker than surface, drying \pm raised, concolorous to weakly paler than surface; midrib round-raised and obtusely minutely many-ribbed on lower surface; **basal veins** 1 to 2 pairs, coalesced into a prominent posterior rib or loosely coalesced, with 4 to 5 branching off, 3 acroscopic, 1 to 2 basisopic, the first free to the base, 3 to 4 fused into a short posterior rib 1–2 cm long; primary lateral veins 4 to 6 pairs, arising at 30°–60°, most acutely toward apex, weakly to moderately arcuate, occasion-

ally straight, round-raised on lower surface; collective veins 3, the innermost arising from one of the lowermost lateral veins on inner side of posterior lobe, loop-connected with all preceding lateral veins, moderately scalloped, 3–14 mm from margin, frequently markedly remote from margin (relative to blade size). INFLORESCENCES erect, 1 to 2 per axile; peduncle held within the sheath, 21–25 cm \times 2–3 mm, as long as or longer than petiole, narrowing toward base, pale green, drying matte to weakly glossy, dark brown; **spathe** erect, ca. 8 cm long, cuspidate at apex, broadly funnel-shaped at anthesis; spathe tube pale green on outer surface, ca. 4 cm \times ca. 6 mm, drying matte, medium-dark brown on outer surface, weakly glossy and weakly paler on inner surface, densely pale, punctiform; spathe blade white, ca. 4 cm \times ca. 6 mm, opening broadly (to 1.3 cm wide) at anthesis, drying matte, medium-dark brown on outer surface, weakly glossy, weakly paler on inner surface, weakly and densely pale, punctiform; **spadix** erect, stipitate 1–1.5 mm, ca. 6.8 cm long, adnate to spathe ca. 1.9 cm at base, along stipe and to slightly more than 1/2 of the length of pistillate portion; pistillate portion green, 3.1 cm \times 3 mm, weakly wider than thick, broadest above middle, drying pale to medium-dark tan; fertile staminate portion bright orange, 2.6 cm \times 4 mm, bluntly acute at apex, broadest near base, weakly tapering, drying medium-dark orangish brown; sterile staminate portion ca. 1.1 cm \times 2.5–3.5 mm, broadest at apex, drying medium orangish brown; pistils weakly coherent, ca. 3 across the axis (viewed from above), ca. 1.5 mm long; ovaries \pm cylindrical (possibly subglobose), 0.8–1 \times 2–2.5 mm, drying medium-dark brown; style Type 9 (Fig. 1), ca. 0.5 \times 1.5–2 mm, comprising 1/3 or slightly less of the length of pistil, most margins weakly coherent with those of adjacent styles; **stigma** 0.5–0.7 mm diam., weakly elevated on and weakly broader than narrowed portion of style (on drying); synandria 1–1.2 \times 2–2.2 mm, coherent, truncate, 3- to 4-lobed, 3- to 4-androus; sterile flowers 0.5–0.7 \times 1–1.5 mm, weakly coherent, truncate, subprismatic, in 6 whorls. INFRUCTESCENCE medium green, ca. 5 cm \times ca. 7 mm, drying matte, medium-dark brown on outer surface, moderately paler on inner surface; berries 2–3.5 mm diam., drying tan.

Phenology. Flowering in *Chlorospatha bogneri* is reported only for the months of June, July, and November. Inflorescences apparently emerge in slow progression, with several days between anthesis of one inflorescence and emergence of the next inflorescence at the apex of the petiole sheath. The

label notes for *Bittner 2493* state that black beetles pollinate this species.

Discussion. *Chlorospatha bogneri* is known only from La Planada Reserve in Nariño Department, in premontane wet forest on the Pacific slope in southern Colombia, at 1700–2050 m elevation and possibly occurs in northern Ecuador, along the border. *Chlorospatha bogneri*, a member of *Chlorospatha* sect. *Occidentales*, is a striking plant with markedly dark green, minutely rugose leaf blades with all orders of venation prominently raised, minutely puberulent to granular-puberulent on the lower surface and darker than the surface. The species is also distinguished by the petiole sheath, which occupies three fourths of to nearly the entire length of the petiole and is free-ending at the apex, conspicuously so when in flower. Commensurate with such extensive sheathing is the long peduncle that is as long as or longer than the petiole, a condition infrequently encountered in *Chlorospatha*. The bright orange synandria are known in only four other species in the genus, all of which occur in the frontier region along the border between Colombia and Ecuador, on the western slopes of the Andes: *C. besseae*, *C. dodsonii*, *C. litensis*, and *C. mansellii*.

Chlorospatha bogneri might be confused with only one species, *C. besseae*, also from the frontier region along the border between Colombia and Ecuador on the Pacific slope, but the latter is known only from Ecuador, at 550–814 m, well below the known elevation of *C. bogneri* (see discussion under *C. besseae*). The two species are possibly closely related.

Additional specimens examined. COLOMBIA. **Nariño:** La Planada, 7 km above Chucunés on Túquerres–Ricaurte rd., trail above La Posada bldg., 1780 m, 1°05'N, 78°01'W, 26 July 1988, *Croat 69556* (MO); La Planada, S of Ricaurte, 7 km from Tumaco–Pasto rd., 1800 m, 1°10'N, 77°58'W, 24 July 1986, *A. Gentry, O. Benavides, G. Castillo & B. Ramirez 55072* (MO); Mpio. Ricaurte, Reserva La Planada, 1800 m, Borde Marcos, 15 Nov. 1993, *C. Restrepo 743* (MO).

8. *Chlorospatha boosii* Croat & L. P. Hannon, sp. nov. TYPE: Ecuador. Morona-Santiago: Limón–El Triunfo rd., 915 m, 3°01'15"S, 78°23'05"W, Mar. 1996, *Croat & L. P. Hannon 81478* (holotype, MO-04901597!; isotypes, AAU!, B!, BR!, CAS!, COL!, CUVCI!, F!, GB!, GH!, HUA!, INB!, K!, M!, MEXU!, NY!, P!, PMA!, QCA!, QCNE!, RSA!, UB!). Figure 9A–D.

Herba 30–50 cm; internodia 0.5–1.5(–2) × 1.7–3.5 cm; cataphylla 12–17 cm longa. Petiolus 24–46.5 cm longus; lamina foliaris ovata, (16–)19–27.5 × (7–)13–19.5 cm, lobis posterioribus (4.5–)6.5–11 × (3.5–)6.5–10 cm, nervis basalibus utroque 1 ad 3, nervis primariis lateralibus

utroque 3 vel 4. Inflorescentiae erectae, 4 ad 7 in quaque axilla; pedunculus 6–12 cm longus; spatha 8–14 cm longa, tubo 0.8–2.5 cm × 3–7 mm; spadix 5.6–6.9 cm longus.

Terrestrial herb, 30–50 cm tall; stem decumbent, erect to 15 cm, remnants of old leaf bases persisting as few short fibers at upper nodes, with bulbils produced randomly along its length; bulbils in rosette clusters of (1–)2–6, 2–5 × 2–4 mm, covered with brownish fibers; sap milky; internodes 0.5–1.5(–2) × 1.7–3.5 cm, weakly glossy to semiglossy, medium to dark green, becoming weakly scurfy and greenish tan with age, with nodes raised and scurfy, drying matte, medium greenish brown to brown; cataphylls quickly deciduous, 12–17 cm long, erect-spreading and loosely arranged, obtuse with acumen (acumen to 1 cm long) or cuspidate at apex, obtusely 1- to 2-ribbed abaxially, weakly glossy, pale green, occasionally irregularly weakly darker green-mottled in narrow transverse bands. LEAVES 8 to 12, erect, erect-spreading, spreading and reflexed-spreading; **petioles** 24–46.5 cm long, glabrous, matte to weakly glossy, medium to dark green, drying matte to weakly glossy, medium to dark green or greenish brown, sheathed 13–30 cm, (1/3 to) 1/2 to 2/3 of total length; sheath decurrent at apex, the sides 5–10 mm wide and spreading to 90° from petiole axis midway, appearing winged; free portion 4–6 mm diam. midway (drying 2–4.5 mm diam.), obtusely D-shaped, with margins becoming bluntly acute in apical 1/4, narrowly, acutely sulcate or bluntly sulcate; **blades** ± erect-spreading to drooping, ovate (occasionally subsagittate in juvenile plants), frequently subhastate on drying, cordate-subcordate at base, subcordate on drying, (16–)19–27.5 × (7–)13–19.5 cm, 1.3 to 1.9 times longer than wide, weakly acuminate or apiculate at apex, broadest at base, (1)1.1 to 1.2 times wider at base than across anterior lobe (measured tip to tip across posterior lobes), occasionally widest midway in juvenile plants, frequently weakly to moderately constricted on one side, occasionally on both sides, thin, moderately to prominently bicolorous; upper surface broadly quilted, velvety (matte-subvelvety), medium to dark green, drying matte to velvety-matte, dark green, frequently narrowly weakly paler along major veins; lower surface reticulate, narrowly minutely colliculate and matte along all venation, otherwise weakly glossy, drying weakly glossy to semiglossy, moderately to conspicuously paler, frequently narrowly and weakly paler along major veins; anterior lobe (14–)17–23.5 × (7–)11.5–17.5 cm, 1.3 to 1.5 times longer than wide, 2.1 to 2.6 times longer than posterior lobes, broadest at or near base, ± symmetrical; posterior lobes directed toward the base or somewhat outward, (4.5–)



Figure 9. A–C. *Chlorospatha boosii* Croat & L. P. Hannon from the type collection Croat & L. P. Hannon 81478 (MO). —A. Potted type plant showing habit. —B. Leaf blade, adaxial surfaces. —C. Close-up of inflorescence showing hooded, recurved spathe. —D. Close-up of inflorescence showing front view of inflorescence with slightly hooded spathe, from Croat & L. P. Hannon 81476 (MO paratype).

6.5–11 × (3.5–)6.5–10 cm, 1 to 1.3 times longer than wide, broadest and occasionally weakly constricted at base, bluntly to narrowly rounded at apex, markedly inequilateral, the inner side always narrower, ± rounded toward base and briefly attenuate onto posterior rib or decurrent onto petiole; outer side 2.5 to 3.5 times wider than inner side midway, ± straight toward base; midrib deeply sunken and concolorous on upper surface, round-raised on lower surface, matte, weakly paler to weakly darker than surface, drying raised, weakly to moderately darker than surface; **basal veins** 1 to 3 pairs, coalesced into a prominent posterior rib or weakly coalesced, with 4 to 8 branching off, 2 to 3 acroscopic, 3 to 4 basiscopic, the first free to the base (or not) and fused 1–5 mm to second and/or third, posterior rib naked 3–9 mm per side, rarely not at all, drying ± flattened, weakly darker than surface; primary lateral veins 3 to 4 pairs, arising at 25°–55°, most acutely toward apex, moderately arcuate, quilted-sunken and concolorous on upper surface, frequently drying weakly glossy, narrowly raised or round-raised and obtusely angular on lower surface, matte, concolorous to weakly paler or weakly darker than surface, drying ± flattened, concolorous to weakly darker than surface; secondary veins in part weakly sunken on upper surface, weakly raised and concolorous on lower surface, drying in part weakly raised, concolorous or weakly paler than surface; tertiary veins in part weakly raised, otherwise prominulous on lower surface, weakly darker than surface, drying mostly flat, distinct, and visible, weakly darker than surface; reticulate veins visible, distinct on lower surface, weakly darker than surface, drying visible, distinct, weakly darker than surface; collective veins 3, the innermost arising from apex of posterior rib, occasionally from uppermost lateral vein on inner side of posterior lobe, loop-connected with all preceding lateral veins, moderately scalloped, 5–10 mm from margin. **INFLORESCENCES** erect, 4 to 7 per axil, emitting a sweet fragrance at anthesis; sympodium held within a sympodial cataphyll; sympodial cataphyll 10–15 × 1–2.5 cm, acuminate at apex, 1- to 2-ribbed abaxially, medium green; inflorescence cataphyll 1- to 2-ribbed abaxially; peduncle 6–12 cm long, cylindroid, 3–5 mm thick, 2 mm wide, or ca. 5 mm diam. and obtusely D-shaped, acutely so near apex, matte to weakly glossy, pale-medium to medium green or yellow-green, drying 1–1.5 mm diam., matte to weakly glossy, medium to dark brown; **spathe** cucullate, frequently prominently so, medium yellow-green to dark green, 8–14 cm long, 2–4(–6) cm longer than spadix, lanceolate, gradually to abruptly acuminate at apex, opening narrowly most of its length at anthesis;

spathe tube matte on outer surface, semiglossy on inner surface, 0.8–2.5 cm × 3–7 mm, thicker than broad, drying 2–4 mm diam., matte (rarely weakly glossy), dark brown or greenish brown; spathe blade matte to weakly glossy, with veins prominulous on outer surface, semiglossy to glossy on inner surface, with veins sunken and weakly darker than surface, 5.5–8.2 cm × 5–7 mm, 2–2.3 cm wide (flattened), drying matte to weakly glossy, medium to medium-dark yellowish green to greenish tan on both surfaces, paler than tube, marcescent, erect after anthesis; **spadix** erect, 5.6–6.9 cm long, sessile, adnate to spathe 3–7 mm at base, 1/4 to ca. 1/2 of the length of pistillate portion; pistillate portion pale yellow to pale yellow-green, 1–1.5 cm × 3–3.5 mm, weakly broadest midway, drying tan; fertile staminate portion matte, whitish to cream, 3.4–4.5 cm × 3.5–4 mm, bluntly acute at apex, broadest near base, weakly tapering, drying brownish cream; sterile staminate portion matte, white to creamy white, 5–9 × 2.5–3 mm, broadest apically, drying brownish; pistils weakly coherent, 2 to 3 across the axis (viewed from above), ca. 1 mm long; ovaries ± cylindrical to obtusely obconical, broadly concave medially, greenish white to pale yellowish green, 1–1.5 mm diam., usually 2-locular with axile or subaxile placentation and 6 to 10 ovules per locule, rarely unilocular with subaxile placentation and 8 ovules, the axis intact; ovules hemianatropous, biseriate; funicles shorter than ovules; style Type 1 (Fig. 1), ca. 1 mm diam., thin, weakly narrower than ovary, the margins distinct and visible; **stigma** white, cream or greenish, 0.3–0.4 mm diam., sessile, coronate, weakly broadest at apex; synandria ca. 1 mm long, 2–2.2 × 1–1.2 mm diam. and ± elongated in direction of axis, occasionally subrounded, occasionally highly bilaterally symmetrical, prominently and deeply (2)3- or 4-lobed (occasionally almost to the middle), coherent, broadly concave medially with lobes thickened, the margins sinuate-undulate and interlocking with margins of adjacent flowers, 3- to 4-androus, the thecae each with a terminal pore; pollen creamy white; sterile flowers ca. 1 mm long, 2–2.2 × 1.3–1.5 mm diam. and ± elongated in direction of axis, subprismatic to irregularly prismatic, densely arranged in 3 to 5 whorls, more laxly in basal whorl. Berries not known.

Phenology. Flowering occurs in *Chlorospatha boosii* only during the months of May through September. Sterile collections were made in March and later flowered in cultivation only during those months. Inflorescences are fragrant and emerge in quick succession, with each reaching anthesis approximately one to three days after anthesis of the preceding inflorescence.

Etymology. *Chlorospatha boosii* is named for Julius Boos (1946–2010), noted Trinidadian naturalist and expert on Araceae, whose unsolicited gift to the second author, of Madison's paper (1981), including his treatment of *Chlorospatha*, ultimately led to the preparation of this revision.

Discussion. *Chlorospatha boosii* is known from tropical moist forest and possibly either premontane moist forest or lower montane moist forest on the eastern slopes of the Andes, to the north and south of Limón in Morona-Santiago Province, Ecuador, at 500–944 m elevation. It is noteworthy that two collections were made on the eastern slopes of the Cordillera de Cutucú, near the border with Peru, suggesting the possibility that *C. boosii* is sympatric with *C. longipoda* and *C. pubescens* in that area. The species would be expected to occur elsewhere in Morona-Santiago and eastward into Peru, also to the south, in Zamora-Chinchipe Province.

Chlorospatha boosii, a member of *Chlorospatha* sect. *Orientales*, is found in small colonies and is distinguished by its broadly quilted, velvety, medium to dark green, broadly ovate leaf blades that are cordate-subcordate at the base, with the posterior lobes broad, more or less rounded at the apex and approximately half as long as the anterior lobe. Although it is a robust plant with stems to 3.5 cm in diameter, it is no more than 50 cm tall and has numerous leaves (eight to 12) that are held erect, erect-spreading, spreading, and reflexed-spreading. The petiole is sheathed (one third to) one half to two thirds of its length, with the sheath distinctive in having sides 5–10 mm wide and broadly flaring (to 90°), thus appearing winged. The species is also distinguished by the absence of cataphylls when not in flower. The peduncles are moderately long (6–12 cm long) and the inflorescence the largest recorded for a species from the eastern slopes, 8–14 cm long. The spathe of *C. boosii* is entirely medium to dark green or yellow-green and moderately to occasionally prominently cucullate, in the latter instance seeming almost deformed, with the apical half of the blade doubled over the spadix and the apex directed downward. The staminate portion of the spadix is matte and cream-colored and the styles, pale yellow to pale yellow-green.

Chlorospatha boosii is probably most closely allied and most easily confused with *C. hannoniae*, with which it is sympatric in Morona-Santiago Province. The two species are similar in several respects, both being relatively short, but somewhat robust, plants with numerous leaves, similar leaf blades, and the same unusual petiole sheathing. The stems of *C. boosii* can be 1 cm wider, with bulbils usually in

clusters of two to six, differing from the usually solitary bulbils observed in *C. hannoniae*. In *C. boosii*, the upper surface of the leaf blade is broadly quilted and velvety, medium to dark green, differing from that of *C. hannoniae*, which is sub-bullate and weakly glossy, dark blackish green. The posterior rib is not naked in the latter species but is usually naked 3–9 mm on each side in *C. boosii*. The peduncle of *C. boosii* is entirely green and usually longer than that of *C. hannoniae*, which is purple-tinged green. The spathe and spadix of *C. boosii* are consistently and significantly longer than those of *C. hannoniae*. The spathe of *C. boosii* is entirely green and 8–14 cm long, with the spadix 5.6–6.9 cm long and adnate to the spathe one fourth to one half of the length of the pistillate portion. *Chlorospatha hannoniae* differs in having the spathe 4.5–6 cm long, the tube purple-tinged green, the blade dark maroon, and the spadix 3.8–5 cm long and adnate only narrowly at the base. The synandria and sterile flowers are matte in *C. boosii* and glossy in *C. hannoniae*. The ovaries in the latter species are white, with the style white and densely dark purple-speckled. The ovaries of *C. boosii* are greenish white to pale yellow-green, with the style pale yellow to pale yellow-green.

Chlorospatha boosii could possibly be confused with *C. longipoda*, which is widespread on the eastern slopes of the Andes in Ecuador, at 470–1700 m elevation, and is probably sympatric with this species in Morona-Santiago Province. *Chlorospatha boosii* is a more robust plant when mature, with stems to 3.5 cm diameter versus 1.3 cm diameter in mature specimens of *C. longipoda*, which retain the remnants of old cataphylls and petiole bases more or less intact, thus differing from *C. boosii* in which these are, for the most part, deciduous. *Chlorospatha longipoda* has three to five erect to erect-spreading leaves, differing from *C. boosii*, which has eight to 12 leaves, the newest erect to erect-spreading, eventually becoming reflexed-spreading as newer growth is made. The mature blades of the latter species are larger as well as wider, with the posterior lobes longer, the anterior lobe being ca. 2.1 to 2.6 times longer than the posterior lobes versus usually ca. 3.5 to 10 times longer in *C. longipoda*. *Chlorospatha boosii* has three or four pairs of primary lateral veins versus four to six pairs in *C. longipoda*. The petiole sheathing is distinctive in *C. boosii*, with the sides broad and flaring, appearing winged. In *C. longipoda*, the sides are narrow and in-rolled or erect with the margins in-rolled. Flowering has been reported in *C. longipoda* during various months and probably occurs throughout the year. Flowering is seasonal in *C. boosii*, occurring only from May through September. It is noteworthy that *C. boosii* usually produces cataphylls

only during the flowering cycle, thus differing from *C. longipoda*, which produces cataphylls with each new vegetative and sympodial growth.

Paratypes. ECUADOR. **Morona-Santiago:** Limón-Méndez rd., 938 m, *Croat & L. P. Hannon 81476* (MO); along Puerto Morona-Santiago rd., at Río Morona, near summit of hills, Km. 18 from Río Morona, 500 m, *Croat 87417* (MO, QCNE); along Santiago-Morona rd. at Río Morona, 23.4 km E of Santiago, 500 m, *Croat 87454* (MO, QCNE); along rd. betw. Santiago & Río Morona, 33.7 km E of Santiago, 523 m, *Croat, L. P. Hannon, G. Walther & K. Tuniak 90681* (MO, QCNE); Patuca-Santiago rd., Cordillera de Cutucú, 11.4 km E of Patuca turn-off on Macas-Limón rd., 5.1 km E of Patuca, 944 m, *Croat, L. P. Hannon, G. Walther & K. Tuniak 90610* (MO, QCNE).

9. *Chlorospatha bullata* Croat & L. P. Hannon, sp. nov. TYPE: Colombia. Valle: Finca Zigara, Elvira distr., Km. 18 on Calí-Buenaventura hwy., Km. 4 via Dapa, 1900 m, 3°30'N, 76°34'W, 2–3 Apr. 1994, *J. Giraldo & C. Espinosa 255* (holotype, MO-05071721!; isotypes, CUVC not seen, TULV not seen). Figure 8C, D.

Herba usque ad 40 cm; internodia (1–)1.5–4 × 0.8–2.5 cm; cataphylla 6–13.5 cm longa. Petiolus (13–)16–34 cm longus; lamina foliaris sagittata, anguste ovato-sagittata vel ovato-sagittata vel anguste triangularis, 16.5–28 × (5.5–)7–13 cm, lobis posterioribus (5–)7–10.5 × (2.5–)2.8–6 cm, nervis basalibus utroque 2 ad 4, nervis primariis lateralibus utroque 3 ad 5. Inflorescentiae erectae, 2 in quaque axilla; pedunculus 8–12 cm longus; spatha erecta, 5.2–8 cm longa; spadix 4.5–6.2 cm longus.

Terrestrial herb, to 40 cm tall; stem decumbent, to 1.5 m long, erect at apex, remnants of old leaf bases and cataphylls persisting intact to semi-intact along its length, rarely weakly fibrous; sap translucent white; internodes (1–)1.5–4 × 0.8–2.5 cm, semiglossy, medium green, drying weakly glossy to semiglossy, medium to dark brown or grayish brown (all measurements made from dried material); cataphylls 6–13.5 cm long, obtuse with acumen at apex (acumen to 3 mm long), drying semiglossy to glossy, rarely weakly glossy, medium-dark reddish brown, weakly fibrous. LEAVES 2 to 4, erect-spreading; **petioles** (13–)16–34 cm long, moderately spongy, glabrous, dark green, ± purple-tinged, drying weakly glossy to semiglossy, dark brown, occasionally almost black, sheathed 8–13 cm, ca. 1/3 of total length (ca. 1/4 of length on foliage leaves); sheath decurrent at apex, rarely free-ending; free portion 2–4 mm diam. midway, terete; **blades** sagittate, narrowly ovate-sagittate or ovate-sagittate or narrowly triangular, somewhat elliptical in larger specimens, 16.5–28 × (5.5–)7–13 cm, 1.5 to 2.5(to 3) times longer than wide, narrowly acuminate at apex, usually broadest midway, occasionally broadest at

base, weakly or not at all constricted in area of petiole attachment, thin, moderately bicolorous; upper surface minutely bullate, matte, dark green, drying minutely bullate, matte (rarely weakly glossy), dark green to brownish green; lower surface prominently reticulate, with areoles deeply sunken, rarely purplish, drying densely reticulate, weakly glossy to semiglossy (rarely matte), weakly to moderately paler, occasionally weakly gray-tinged, rarely weakly purplish; anterior lobe 11–17.4 × 5.5–13 cm, 1.5 to 2(to 2.2) times longer than wide, 1.5 to 2(to 2.5) times longer than posterior lobes, broadest at or near base, occasionally midway, ± symmetrical; posterior lobes directed somewhat outward, (5–)7–10.5 × (2.5–)2.8–6 cm, 1.6 to 2.5 times longer than wide, narrowly rounded to occasionally bluntly rounded at apex, usually broadest at base, moderately to markedly inequilateral, the inner side narrower, frequently overlapping with that of opposite lobe, ± rounded toward base, briefly to gradually attenuate and decurrent onto petiole, possibly weakly confluent with opposite lobe, the confluent portion obscuring apex of petiole; outer side 1.7 to 3.8 times wider than inner side midway, ± straight or weakly concave to convex toward base; all orders of venation narrowly sunken on upper surface, usually drying weakly glossy and weakly paler than surface (creating a fine, netlike pattern), prominently raised and granular-puberulent on lower surface; midrib round-raised on lower surface, paler than surface, drying raised to weakly flattened, concolorous to weakly paler than surface, rarely weakly darker; **basal veins** 2 to 4 pairs, coalesced into a prominent posterior rib; primary lateral veins 3 to 5 pairs, arising at 30°–85°(–90°), frequently markedly arcuate, occasionally weakly arcuate or irregularly ascending (rarely straight), round-raised to convex on lower surface, paler than surface, drying raised to weakly flattened, concolorous to weakly paler than surface, rarely weakly darker; minor venation drying raised on lower surface, concolorous to weakly paler than surface; collective veins 3 to 4, the innermost arising from one of the basal veins on outer side of posterior lobe (usually the uppermost) or from apex of posterior rib, loop-connected with all preceding lateral veins, rarely with the 2 primary lateral veins toward the apex (of anterior lobe) disconnected and markedly arcuate to the margin at the apex or onto the midrib, ± scalloped, occasionally markedly scalloped, 0.3–1.7 cm from margin. INFLORESCENCES erect, 2 per axil; peduncle held within the sheath, 8–12 cm × 1 mm, glabrous, medium green, weakly irregularly darker-mottled in narrow transverse bands, drying weakly glossy, medium to dark brown; **spathe** erect,

5.2–8 cm long, acuminate at apex, the margins in-rolled in apical 3 mm; spathe tube medium green on outer surface, 2.5–4 cm \times 2–5 mm, drying matte to weakly glossy, dark brown on outer surface, weakly glossy and weakly paler on inner surface; spathe blade white, 2.7–4 cm long, 1.5 cm wide (flattened), drying weakly glossy, medium to medium-dark reddish brown on both surfaces, weakly paler than tube, marcescent, erect after anthesis; **spadix** erect, 4.5–6.2 cm long, sessile, adnate to spathe 2.2–2.4 cm at base, the entire length of pistillate portion and to 2 mm of sterile staminate portion; pistillate portion purplish, 2–2.2 cm \times 2–3 mm; fertile staminate portion creamy white, 1.9–3 cm \times 2.5–4.5 mm, narrowly rounded to bluntly acute at apex, \pm cylindrical or tapering, drying dark brown; sterile staminate portion 0.6–1.2 cm \times ca. 1.7 mm, \pm cylindrical, drying medium to dark brown; pistils weakly coherent, ca. 3 across the axis (viewed from above), ca. 1.2–1.75 mm long; ovaries subglobose, 1–1.2 \times 1.5–2 mm, drying medium to dark tan; style Type 9 (Fig. 1), ca. 0.6 \times ca. 1–2 mm, comprising ca. 1/3 of the length of pistil, most margins weakly coherent with those of adjacent styles; **stigma** weakly elevated on style, drying tan; synandria 1–1.2 \times 1–1.5 mm, coherent, truncate, deeply 3- to 4-lobed, 3- to 4-androus (mostly 4); sterile flowers less than 1 mm long, 1.2–2 \times 1 mm diam. and \pm elongated in direction of axis, irregularly lobed (margins narrowly sinuate), laxly arranged to weakly coherent, in 3 to 5 whorls. Berries not known.

Phenology. Flowering is only known to occur in *Chlorospatha bullata* during the months of April and July.

Etymology. The epithet of the new species is taken from the Latin “bullatus,” meaning “bullate,” “blistered,” or “puckered.”

Discussion. *Chlorospatha bullata* is known only from premontane rainforest, premontane moist forest, and possibly either premontane wet forest or lower montane wet forest on the eastern and western slopes of the Cordillera Occidental in Valle Department, Colombia, at 1020–2000 m elevation.

Chlorospatha bullata is a member of *Chlorospatha* sect. *Occidentales* and is distinguished by its moderately long internodes, purple-tinged petioles, and thin, sagittate, narrowly ovate-sagittate, or triangular leaf blades that are matte and minutely bullate on the upper surface and densely reticulate, with deeply sunken areoles on the lower surface, which is usually green but can rarely be purplish. The blades dry green, with all venation paler than the

upper surface and the surface itself rough to the touch, a condition not observed in any other species. It is also distinguished by its short peduncle and small inflorescence with purplish styles.

Chlorospatha bullata could not be easily confused with any species, but could possibly be confused with *C. congensis* from Cauca Department in southern Colombia (see discussion under *C. congensis*).

Paratypes. COLOMBIA. **Valle:** along Calí–Buenaventura hwy. at Km. 20.5, just beyond summit of rd. W of Diez y Ocho, 1930–2000 m, *Croat 38533A* (MO); near Queremal, Estación Microndas Tokio, along old rd. to Buenaventura, *Croat 50130* (MO), *50189* (MO); vic. Dapa, NW of Calí, along Continental Divide, 2000 m, *Croat 61421* (MO); along gravel rd. from Km. 18 on Calí–Buenaventura hwy. to Dapa, 1020 m, *Croat & J. Watt 70520* (CUVC, MO); Calí–Buenaventura Hwy., Km. 29, 1 km E of turnoff to Queremal, 1900 m, 3°30′50″N, 76°36′30″W, 10 July 1997, *Croat & J. Gaskin 79637* (CUVC, MO); La Cumbre, W Cordillera, 1700–2100 m, 9, 11 & 18 Sep. 1922, *T. Hazen & E. Killip 11153* (GH, NY, US).

10. *Chlorospatha caldasensis* Croat & L. P. Hannon, sp. nov. TYPE: Colombia. Caldas: Manizales, Monteleón, Cordillera Central, 2250 m, 12 May 1984, *M. de Fraume & A. Gallego 215* (holotype, MO-3400353!; isotype, FAUC not seen). Figure 10A.

Herba 1.8–2 m; internodia 1.5–2 \times 1.5–1.8 cm. Petiolus ultra 40 cm longus; lamina foliaris profunde 5-loba, ca. 42 \times 42 cm, lobo medio ca. 30 \times 17 cm, confluyente cum lobis lateralibus, nervis primariis lateralibus utroque ca. 5. Inflorescentiae erectae, 1 in quaque axilla; pedunculus ca. 28 cm \times ca. 2 mm; spathae tubo ca. 6.5 cm \times 7 mm.

Terrestrial herb, 1.8–2 m tall; stem with remnants of old cataphylls persisting as numerous linear fibers at upper nodes; internodes 1.5–2 \times 1.5–1.8 cm, drying matte, dark brown (all measurements made from dried material); cataphylls (total length and apex not known) more than 25 cm long, drying semi-intact, moderately fibrous, semiglossy, medium reddish brown. LEAVES 2; **petioles** (total length not known) more than 40 cm long, brown, glabrous, drying weakly glossy to semiglossy, medium to dark reddish brown, weakly fibrous (fibers paler), sheathed ca. 30 cm; sheath apex not known; free portion 2–3 mm diam. midway; **blades** deeply 5-lobed, ca. 42 \times ca. 42 cm, as long as wide, drying thinly coriaceous, moderately bicolorous; upper surface brown, white maculate, drying weakly glossy to semiglossy, dark brown, the maculations not visible (on drying); lower surface drying semiglossy; **medial lobe** in part known, ca. 30 \times 17 cm, 1.8 times longer than wide, about same length as innermost lateral lobes, apex not known, weakly broadest above middle, promi-

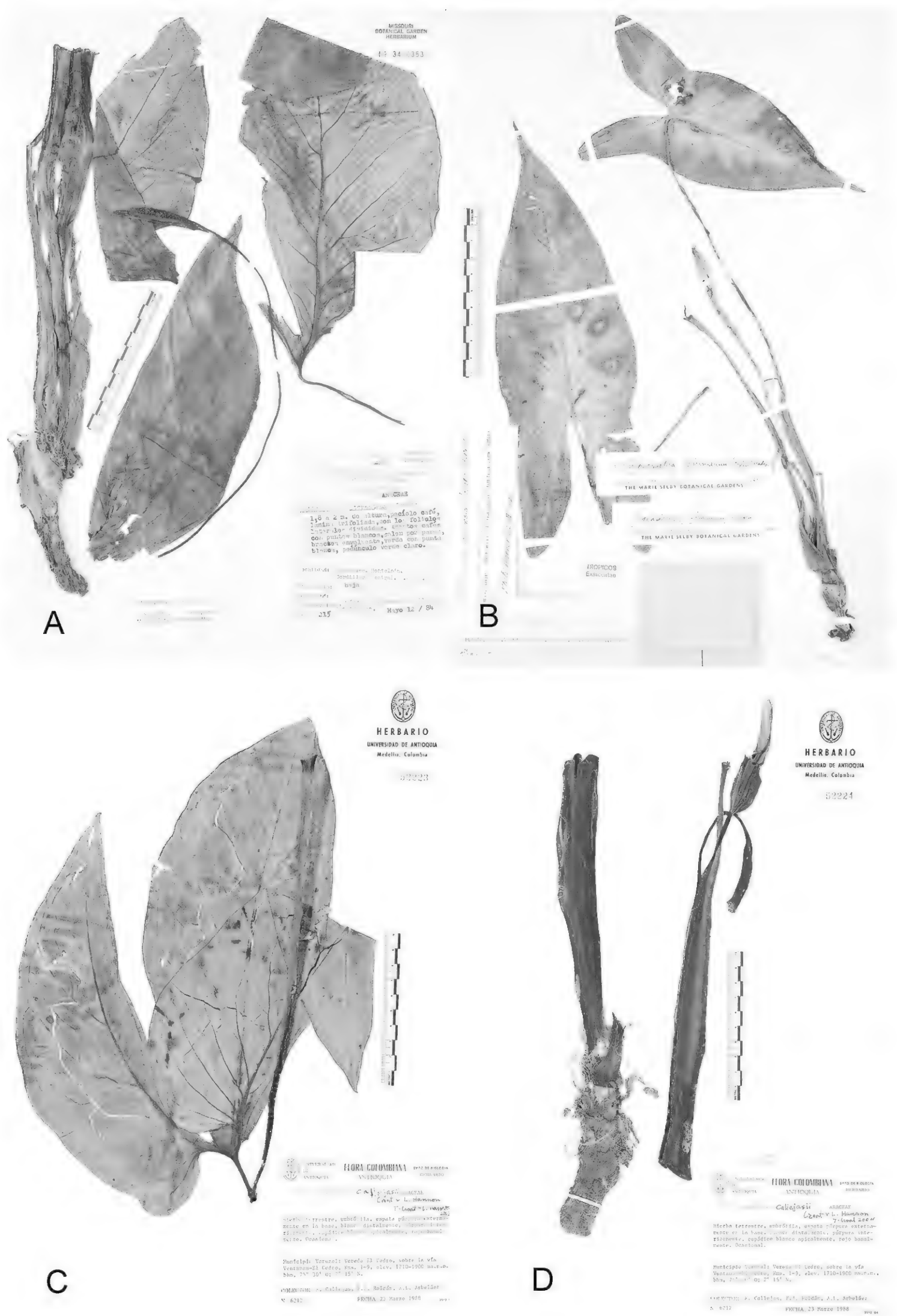


Figure 10. —A. *Chlorospatha caldasensis* Croat & L. P. Hannon, *Fraume & Gallego* 215 (MO holotype). —B. *Chlorospatha caliensis* Croat & L. P. Hannon, *Lehmann* 5384 (K holotype). C, D. *Chlorospatha callejasii* Croat & L. P. Hannon, *Callejas et al.* 6212 (HUA holotype, two sheets). —C. Leaf blade. —D. Stem with petiole and inflorescence.

nently attenuate toward and narrowly attached at base, ca. 2 cm wide at point of attachment; **lateral lobes** confluent with all adjacent lobes, the confluent portion 1.5–2.5 cm wide; innermost segment ca. $30 \times$ ca. 14 cm, apex not known, 2.1 times longer than wide, broadest midway, narrowly attached at base, ca. 2.5 cm wide at point of attachment, moderately inequilateral, the inner side narrower, \pm straight toward base; outer side to 1.5 times wider than inner side midway, \pm acute toward base; outermost segment ca. 20×10 cm, ca. 2 times longer than wide, bluntly acute at apex, broadest below middle, narrowly attached at base, ca. 2 cm wide at point of attachment, inequilateral, the inner side narrower, weakly attenuate toward base; outer side to 2 times wider than inner side midway, \pm acute toward base, narrowly attenuate onto posterior rib; all venation (except reticulate) drying glabrous or in part weakly granular-puberulent on lower surface; midrib and major veins round-raised on lower surface, drying \pm flattened, much darker than surface, almost black; posterior rib naked 2–3 cm per side; primary lateral veins (on medial lobe) ca. 5 pairs, arising at 30° – 40° , \pm straight; primary lateral veins (on lateral lobes) 7 to 8 pairs on innermost segment, arising at 40° – 50° , \pm straight, 5 pairs on outermost segment, arising at 20° – 40° , \pm straight; secondary veins drying raised on lower surface, moderately darker than surface; tertiary veins drying in part prominulous on lower surface, otherwise flat, moderately darker than surface; reticulate veins drying in part visible on lower surface, weakly darker than surface; collective veins 3, the innermost arising from lowermost lateral vein at the base, loop-connected with all preceding lateral veins, markedly scalloped on all segments, 0.8–2 cm from margin. **INFLORESCENCE** erect, 1 per axil; peduncle held within the sheath, $28 \text{ cm} \times$ ca. 2 mm, pale green, drying weakly glossy, dark blackish brown; **spathe** (total length not known); spathe tube green, $6.5 \text{ cm} \times$ ca. 7 mm, drying matte, blackish brown on outer surface, weakly glossy on inner surface, paler and densely tan, punctiform (speckles regularly rounded, appearing as subepidermal cellular inclusions); spathe blade white, otherwise not known; **spadix** erect, total length not known, sessile, adnate to spathe ca. 3 cm at base, ca. 1/2 of the length of pistillate portion; pistillate portion $5.5 \text{ cm} \times$ ca. 5 mm, broadest midway, drying dark reddish brown; fertile staminate portion not known; sterile staminate portion in part known, ca. 2.5 mm diam. at base, drying orangish tan; pistils weakly coherent, 3 to 5 across the axis (viewed from above), 1.5–2 mm long; ovaries \pm cylindrical to obtusely conical, 1.5–2 mm diam., drying medium brown with

darker veins; style Type 3 (Fig. 1), 1–1.5 mm diam.; **stigma** sessile, ca. 3 mm diam.; synandria not known; sterile flowers in part known, ca. 1 mm long, 2×1 mm diam. and elongated in direction of axis, coherent, truncate, irregularly subprismatic. Berries not known.

Phenology. Flowering in *Chlorospatha caldasensis* is known from a single collection that flowered in the month of May.

Etymology. *Chlorospatha caldasensis* is named for Caldas Department, Colombia, in which the type of the new species was collected.

Discussion. *Chlorospatha caldasensis* is known only from the type collection made in lower montane wet forest on the western slopes of the Cordillera Central in Caldas Department, Colombia, at 2250 m elevation. *Chlorospatha caldasensis* is a member of *Chlorospatha* sect. *Chlorospatha* and is unique in the genus in having brown and functional leaves on the living plant. The species is distinguished by its deeply 5-lobed, white maculate leaf blades that are broadly confluent between all segments and dry semiglossy on the lower surface, with the major venation almost black. The species is also distinguished by its relatively long pistillate spadix, 5.5 cm long.

Chlorospatha caldasensis could be confused with *C. luteynii*, which occurs at similar elevations to the north, in the Cordillera Central in Antioquia Department, Colombia (see discussion under *C. luteynii*). *Chlorospatha caldasensis* is a larger plant, 1.8–2 m tall, compared to *C. luteynii*, which is about 1 m tall. The leaves of the latter species are green, with pale yellowish green maculate and dark green blades, differing from those of *C. caldasensis*, which are brown with white maculae. There are four or five pairs of primary lateral veins on the innermost lateral segments of *C. luteynii* versus seven or eight pairs in *C. caldasensis*. The petiole of the latter species dries intact, weakly fibrous, and medium-dark brown, whereas that of *C. luteynii* dries almost black, with the epidermis partially separated, semi-transparent, and semiglossy. The spathe of the latter species is entirely pale green, differing from that of *C. caldasensis*, which has a green tube and white blade.

Grayum (1986) predicted that *Chlorospatha croatiana* subsp. *croatiana*, known only from Central America, at 200–1173(–1400) m elevation, would ultimately be found in Colombia, and although that species and *C. caldasensis* have 5-lobed leaf blades, *C. caldasensis* should be considered distinct (see discussion under *C. croatiana* subsp. *croatiana*). It

differs from *C. croatiana* subsp. *croatiana* in having brown leaves with white maculae in living material. A sterile collection of what is presumably *C. croatiana* subsp. *croatiana*, made in Costa Rica, is the only collection of this taxon known to have maculate blades and only one blade is weakly pale yellow maculate, the other blades being entirely green. However, maculations are not a consistent character in some species of *Chlorospatha* and occasionally are not visible on drying. Numerous specimens of the latter species were examined in the course of this treatment and the spadices were consistently comparatively short, 3.9–8 cm long. The longer pistillate spadix of *C. caldasensis* would suggest total spathe and spadix lengths are significantly greater than those found in *C. croatiana* subsp. *croatiana*. This holds true also for *C. croatiana* var. *enneaphylla*, a 5- to 9-lobed taxon that occasionally has maculate leaf blades; however, none of the Colombian collections of variety *enneaphylla* are less than 7- to 9-lobed (see discussion under *C. croatiana* var. *enneaphylla*).

11. *Chlorospatha caliensis* Croat & L. P. Hannon, sp. nov. TYPE: Colombia. Valle: W Andes of Calí, 1800–2200 m, s.d., *C. Lehmann 5384* (holotype, K!). Figure 10B.

Herba minus quam 50 cm; internodia 0.9–1.7 cm \times 5–8 mm; cataphylla ca. 10–13 cm longa. Petiolus 29.5–33.3 cm longus; lamina foliaris triangulo-sagittata vel sagittata, 18–26.3 \times 7.5–9.5 cm, lobis posterioribus (6–)6.8–9 \times 2.5–3.5 cm. Inflorescentiae erectae, 2 in quaque axilla; pedunculus 9–13.5 cm \times ca. 1.5 mm; spatha erecta, ca. 7.3 cm longa, tubo ca. 3.6 cm \times 4.5 mm, lamina ca. 3.7 cm \times 6 mm; spadix erectus, ca. 6.5 cm longus.

Terrestrial herb, less than 50 cm tall; stem with remnants of old cataphylls persisting \pm intact at upper nodes; internodes 0.9–1.7 cm \times 5–8 mm, drying wrinkled, weakly glossy, pale tan (all measurements made from dried material); cataphylls ca. 10–13 cm long (apex not known), drying semi-glossy, medium reddish brown. LEAVES 2 to 3, erect-spreading; **petioles** 29.5–33.3 cm long, drying glabrous, weakly glossy, medium reddish brown, sheathed ca. 12 cm, less than 1/2 of total length; sheath decurrent at apex; free portion ca. 2 mm diam. midway, possibly flattened adaxially, with medial rib; **blades** triangular-sagittate to sagittate, 18–26.3 \times 7.5–9.5 cm, 1.9 to 3.5 times longer than wide, long-acuminate at apex, broadest at base, 1 to 1.3 times wider at base than across anterior lobe (measured tip to tip across posterior lobes), weakly or not at all constricted in area of petiole attachment, drying thin, weakly bicolorous; upper surface drying matte, discolorous, weakly medium pinkish tan along major

veins, otherwise darker medium brown; lower surface drying weakly glossy, discolorous, pinkish tan along major veins, otherwise darker, weakly pink-tinged brown; anterior lobe 12.7–18.5 \times 6.6–8.2 cm, 1.9 to 2.3 times longer than wide, 2 to 2.2 times longer than posterior lobes, broadest near base; posterior lobes directed toward the base or weakly outward, (6–)6.8–9 \times 2.5–3.5 cm, 2.3 to 2.7 times longer than wide, narrowly rounded to bluntly rounded at apex, broadest at or near base, moderately inequilateral, the inner side narrower, \pm rounded toward base and briefly attenuate onto posterior rib; outer side 1.5 to 2 times wider than inner side midway; midrib and major venation drying raised on lower surface, weakly darker than surface; midrib round-raised on lower surface; **basal veins** 3 pairs, coalesced into a prominent posterior rib; posterior rib naked 6–7 mm per side; primary lateral veins 4 to 6 pairs, arising at 35°–45°, most acutely toward apex, moderately arcuate; secondary veins drying raised on lower surface, weakly darker than surface; tertiary veins drying in part raised, otherwise prominulous on lower surface, weakly darker than surface; reticulate veins drying in part prominulous on lower surface, otherwise visible, flat, weakly darker than surface; collective veins 4, the innermost arising from one of the lateral veins on inner side of posterior lobe, \pm scalloped, 4–8 mm from margin. INFLORESCENCES erect, to 2 per axil; peduncle held within the sheath, 9–13.5 cm \times 1.5 mm, drying pale tan; **spathe** erect, 7.3 cm long, cuspidate at apex; spathe tube 3.6 cm \times 4.5 mm, drying matte, pale tan on outer surface; spathe blade 3.7 cm \times ca. 6 mm, drying matte, pale tan on both surfaces, marcescent, erect after anthesis; **spadix** erect, 6.5 cm long, sessile, adnate to spathe ca. 3 cm at base, the entire length of pistillate portion and narrowly onto sterile staminate portion; pistillate portion 2.8 cm \times ca. 2 mm, drying medium brownish; fertile staminate portion 2.2 cm \times ca. 2 mm, abruptly acute at apex, \pm cylindrical, drying dark reddish brown, weakly paler at apex; sterile staminate portion ca. 8 \times 1.5–2 mm, broadest apically, with axis naked 1 mm at base, drying dark reddish brown; pistils weakly coherent, 2 to 3 across the axis (viewed from above), 2.2–3 mm long; ovaries subglobose, obtusely truncate at apex, 1–1.2 \times ca. 2 mm, drying cream-colored, with numerous brown veins; style Type 7 (Fig. 1), 2 \times ca. 1–1.3 mm, comprising 1/2 to 2/3 of the length of pistil, the margins probably \pm coherent with those of adjacent styles; **stigma** \pm capitate, markedly elevated on style; synandria ca. 1 \times 1–1.2 mm, coherent, truncate, deeply (2)3- to 4-lobed, (2)3- to 4-androus; sterile flowers 1–1.5 \times ca. 1 mm, weakly coherent and irregularly branched in apical 2

whorls, laxly arranged and fungiform (like toadstools) in basal whorls, in 4 to 5 whorls. Berries not known.

Phenology. Flowering is only known to occur in *Chlorospatha caliensis* sometime between July and March.

Etymology. *Chlorospatha caliensis* is named for the city of Calí, Colombia, mentioned on the label notes of the single collection of the new species.

Discussion. *Chlorospatha caliensis* is known only from the type, a single specimen collected by Lehmann, in what is probably either premontane wet forest or lower montane wet forest on the western slopes of the Cordillera Occidental in Valle Department, Colombia, at 1800–2200 m elevation. Although no date is indicated for the collection, Lehmann died in 1903; therefore, the collection was made in or prior to 1903.

Chlorospatha caliensis is a member of *Chlorospatha* sect. *Occidentales* and is distinguished by its triangular-sagittate to sagittate leaf blades that dry thin and discolorous pinkish tan along the major veins on both surfaces, with the posterior lobes more or less rounded at the apex. All venation dries either raised or prominulous on the lower surface, with most reticulate venation prominulous but with some veins flattened. The species is also distinguished by its short peduncle (9–13.5 cm long), small inflorescence with the spathe less than 8 cm long, and its prominently attenuated style that comprises one half to two thirds of the length of the pistil.

Chlorospatha caliensis could possibly be confused with *C. lehmannii*, which also occurs on the western slopes in Colombia but to the south in Cauca Department. *Chlorospatha lehmannii* differs in having a free-ending petiole sheath and coriaceous, subhastate leaf blades that dry matte on both surfaces, with all venation except the midrib flattened on the lower surface, and the posterior lobes longer (3 or 4 times longer than wide) and acute at the apex. In *C. caliensis*, the sheath is decurrent and the blades sagittate, drying thin and weakly glossy on the lower surface, with most venation raised or prominulous and the posterior lobes less than 3 times longer than wide and more or less rounded at the apex. The blades of *C. caliensis* dry discolorous pinkish tan along the major veins on both surfaces, otherwise medium brown, whereas those of *C. lehmannii* dry dark brown on the upper surface, moderately paler on the lower surface, and not at all discolorous on either surface. The peduncle of *C. lehmannii* is 20–27 cm long and the spathe, 10.5–11 cm long, whereas in *C. caliensis*, the peduncle is less than 14 cm long and

the spathe, less than 8 cm long. The fertile staminate portion of the spadix is cylindrical and only 2.2 cm long in *C. caliensis* and the pistillate portion is also short, 2.8 cm long, with weakly coherent pistils. In *C. lehmannii*, the fertile staminate portion is clavate and more than 3 cm long and the pistillate portion is more than 3 cm long, usually about 5 cm long, with laxly arranged pistils. The synandria of *C. caliensis* are 2- to 4-androus and dry dark, purplish brown, differing from those of *C. lehmannii*, which are 3- to 5-androus and dry medium grayish brown.

Chlorospatha caliensis might be confused with *C. congensis* from Cauca Department, Colombia, which has similarly shaped leaf blades and short peduncles but differs in having blades that dry subcoriaceous and weakly bullate on the upper surface, not at all discolorous on either surface and posterior lobes that are decurrent onto the petiole. In *C. caliensis*, the blades dry thin and smooth on the upper surface and discolorous on both surfaces, with the posterior rib naked. *Chlorospatha congensis* differs also in having the midrib and major and secondary veins wrinkled and more prominently raised on the lower blade surface. The venation is not wrinkled in *C. caliensis*. The style of *C. caliensis* (Type 7, Fig. 1) comprises one half to two thirds of the length of the pistil, differing from that of *C. congensis* (Type 10, Fig. 1), which comprises only one third of the length. The sterile flowers of the latter species are subprismatic, differing from the somewhat fungiform to irregularly branched flowers found in *C. caliensis*.

12. *Chlorospatha callejasii* Croat & L. P. Hannon, Aroideana 27: 11. 2004. TYPE: Colombia. Antióquia: Mpio. Yarumal, vic. El Cedro, betw. Ventanas & El Cedro, Km. 1–9, 1710–1900 m, 7°15'N, 75°30'W, 23 Mar. 1988, R. Callejas, F. Roldán & A. Arbeláez 6212 (holotype, HUA sheet 1: HUA-52223 and sheet 2: HUA-52224!). Figures 10C, D, 11A.

Terrestrial herb, ca. 1 m tall; stem with remnants of old cataphylls persisting in part semi-intact at upper nodes, otherwise as pale, reddish brown, linear fibers (all measurements made from dried material); internodes 1.5–2.5 × 1.5–2.5 cm, drying weakly glossy, medium-dark brown; cataphylls not known. LEAVES 2, probably erect-spreading; **petiole** 82.5 cm long, drying glabrous, weakly glossy, dark reddish brown, almost black, sheathed 45 cm, slightly more than 1/2 of total length; sheath decurrent at apex; free portion ca. 5 mm diam. midway; **blade** deeply 3-lobed, nearly trisect, ca. 33 × ca. 30 cm, 1.1 times longer than wide, drying thinly coriaceous, weakly bicolorous; upper surface green, drying matte-

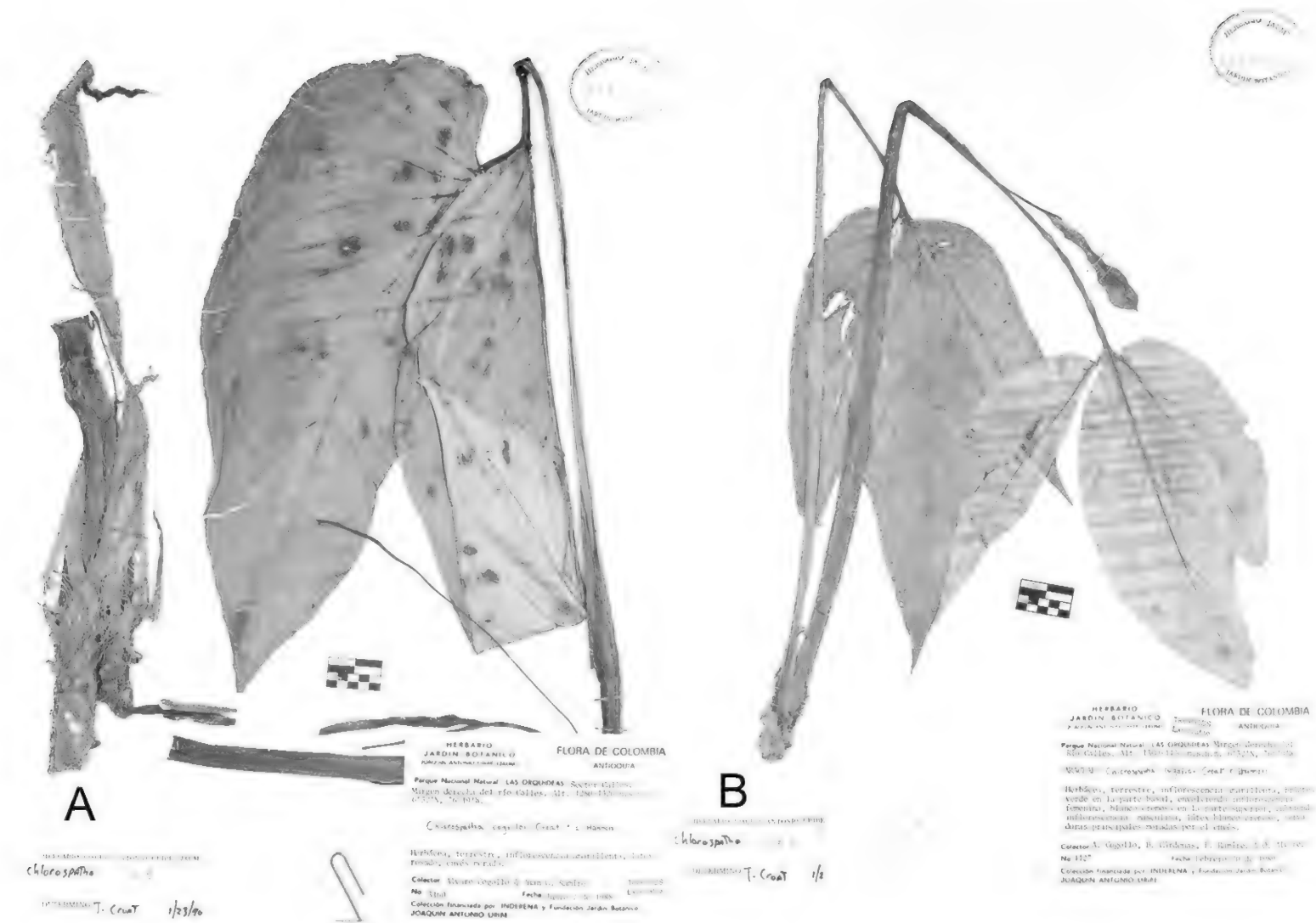


Figure 11. —A. *Chlorospatha cogolloi* Croat & L. P. Hannon, the paratype *Cogollo & Ramírez 3160* (JAUM-16943). —B. *Chlorospatha cogolloi*, the paratype *Cogollo et al. 4127* (JAUM-16946).

subvelvety, weakly green-tinged, dark reddish brown; lower surface drying semiglossy; **medial lobe** 29.5×12 cm, 2.5 times longer than wide, acute at apex, broadest at or above middle, 1.1 to 1.2 times longer than lateral lobes, cuneate and broadly attached at base, ca. 3 cm. wide at point of attachment, weakly inequilateral; **lateral lobes** weakly falcate, directed toward apex, $24.5\text{--}28 \times 8.5\text{--}9.2$ cm, 3 times longer than wide, acute at apex, broadest below middle, markedly inequilateral, the inner side always narrower, weakly attenuate to long-attenuate toward base, narrowly confluent with medial lobe, the confluent portion ca. 4 mm wide; outer side 3.2 to 4.8 times wider than inner side midway, moderately to narrowly rounded at base, briefly attenuate onto posterior rib; midrib and major venation convex on lower surface, drying \pm flattened, much darker than surface, almost black; posterior rib naked 1–1.5 cm per side; primary lateral veins (on medial lobe) 5 pairs, arising at $35^{\circ}\text{--}45^{\circ}$, weakly arcuate; primary lateral veins (on lateral lobes) 9 to 11 pairs, arising at $40^{\circ}\text{--}120^{\circ}$, weakly arcuate, aggregated toward the base, the basal 3 fused near base; secondary veins drying in part weakly raised, otherwise prominulous on lower surface, much darker than surface; tertiary and reticulate veins drying weakly prominulous on

lower surface, weakly darker than surface; collective veins 3, the innermost arising from one of the lowermost lateral veins at the base, loop-connected with all preceding lateral veins, moderately scalloped, 5–10 mm from margin. **INFLORESCENCES** erect, to 2 per axil; peduncle held within the sheath, $46 \text{ cm} \times 2\text{--}3 \text{ mm}$, drying weakly glossy, blackish brown; **spathe** erect, ca. 9 cm long, apex not known; spathe tube dark purple on both surfaces, $4.2 \text{ cm} \times 7 \text{ mm}$, drying weakly glossy, weakly purple-tinged dark brown on both surfaces; spathe blade white, ca. $4.5 \text{ cm} \times 8 \text{ mm}$, drying matte, pale tan, marcescent, erect after anthesis; **spadix** erect, 8.2 cm long, sessile, adnate to spathe ca. 1.5 cm at base, ca. 1/2 of the length of pistillate portion; pistillate portion red, $3.6 \text{ cm} \times 3\text{--}4 \text{ mm}$, broadest below middle; fertile staminate portion white, $3.2 \text{ cm} \times 3.5\text{--}6 \text{ mm}$, broadest near base, weakly tapering, narrowly rounded at apex, drying medium yellowish brown; sterile staminate portion $1.4 \text{ cm} \times \text{ca. } 3 \text{ mm}$, \pm cylindrical, drying medium-dark reddish brown, weakly darker than fertile staminate portion; pistils \pm densely arranged, 4 across the axis (viewed from above), ca. 1 mm long; ovaries cylindrical, $1\text{--}1.5 \times 1\text{--}1.5 \text{ mm}$, drying dark tan with darker veins; style Type 3 (Fig. 1), 1–1.5 mm diam., the margins not

coherent with those of adjacent styles; **stigma** sessile, ca. 0.2 mm diam., \pm capitate; synandria ca. $1 \times$ ca. 1.5 mm, coherent, truncate, deeply 3- to 4-lobed, 3- to 4-androus; sterile flowers ca. 0.5 mm long, $2-3 \times 1$ mm diam. and markedly elongated in direction of axis, coherent, truncate, irregularly prismatic to subprismatic, in 5 whorls. INFRUCTESCENCE (immature) $5.5 \text{ cm} \times 8 \text{ mm}$, drying matte, blackish brown; berries not known.

Phenology. Flowering is only known to occur in *Chlorospatha callejasii* in the month of March.

Discussion. *Chlorospatha callejasii* is known only from the type collection made in premontane wet forest near Yarumal in Antioquia Department, Colombia, at 1710–1900 m elevation in the region of the Magdalena River drainage at the northern end of the Cordillera Central. The species is a member of *Chlorospatha* sect. *Chlorospatha* and is distinguished by its entirely green, nearly trisect leaf blades that dry matte-subvelvety, dark reddish brown on the upper surface and glossy below, with the major and secondary venation almost black, and all segments acute at the apex. It is also distinguished by its dark purple spathe tube and red styles.

Chlorospatha callejasii is one of only three trilobed species occurring in the region east of the Cordillera Occidental in Colombia, and it might be confused with only one of these, *C. betancurii* (see discussion under *C. betancurii*).

It could be argued that *Chlorospatha callejasii* is possibly conspecific with *C. mirabilis*, since in one specimen of the latter species (*Hort. Veitch s.n.*) from an undetermined locality, the inner surface of the spathe tube is purple. However, all known Colombian collections of *C. mirabilis* are from the western slopes of the Andes at lower elevations. These, including the specimen of undetermined origin for *C. mirabilis*, differ from *C. callejasii* in having the upper blade surface drying somewhat glossy and the lower blade surface and petiole purple or purplish green. *Chlorospatha callejasii* is entirely green, with the upper blade surface drying matte-subvelvety. There are fewer pairs of primary lateral veins on the lateral segments in *C. mirabilis*, three to six versus nine to 11 in *C. callejasii*. The sterile staminate portion of the spadix comprises about one third of the total length in *C. mirabilis*, with the flowers laxly arranged in seven to nine(to 11) whorls, but comprises only one fifth of the total length in *C. callejasii*, with the flowers densely arranged in five whorls.

13. *Chlorospatha carchiensis* Croat & L. P. Hannon, sp. nov. TYPE: Ecuador. Carchi: vic. Maldona-

do, 1800 m, 15 Apr. 1977, *M. Madison 3988* (holotype, US!; isotype, SEL!). Figure 12A.

Herba ca. 1.5 m; internodia $1.7-3 \times 1.5-2 \text{ cm}$; cataphylla 22–31 cm longa. Petiolus 36.5–75.5 cm longus, vaginatus per 19–44 cm; lamina foliaris sagittata, $21-36.5 \times 12-20 \text{ cm}$, lobis posterioribus $7.5-17 \times 3.5-8 \text{ cm}$, nervis basalibus utroque 5 vel 6, nervis primariis lateralibus utroque 4 vel 5. Inflorescentiae 1 ad 3 in quaque axilla; pedunculus $27-33 \text{ cm} \times 2-4 \text{ mm}$; spatha erecta, 10.7–11.5 cm longa, tubo 4–6 cm \times ca. 5 mm, lamina ca. $5.5 \text{ cm} \times 5 \text{ mm}$; spadix 9.5–10.8 cm longus.

Terrestrial herb, ca. 1.5 m tall; stem decumbent, erect to 60 cm, with remnants of old leaf bases and cataphylls persisting \pm intact at upper nodes; internodes $1.7-3 \times 1.5-2 \text{ cm}$, drying matte to weakly glossy, dark brown or green (all measurements made from dried material); cataphylls 22–31 cm long, obtuse with acumen at apex, drying semiglossy, dark reddish brown. LEAVES 1 to 2, erect-spreading; **petioles** 36.5–75.5 cm long, glabrous, drying matte to weakly glossy, dark reddish brown, sheathed 19–44 cm, 1/2 to slightly more of total length; sheath free-ending at apex; free portion 2–5 mm diam. midway; **blades** sagittate, occasionally \pm triangular, $21-36.5 \times 12-20 \text{ cm}$, 1.8 to 2.8 times longer than wide, abruptly to gradually acuminate at apex, broadest at base, 1.1 to 1.2 times wider at base than across anterior lobe (measured tip to tip across posterior lobes), thin, moderately bicolorous, weakly to moderately constricted on one side in area of petiole attachment, markedly constricted on opposite side, 1–3 cm narrower at point of constriction; upper surface drying matte to weakly glossy, medium-dark to dark green or brownish green; lower surface drying (weakly glossy) semiglossy, weakly to moderately paler; anterior lobe $14.5-22.5 \times 6-14.5 \text{ cm}$, 1.5 to 2.2 times longer than wide, 1.3 to 1.8 times longer than posterior lobes, broadest near base, weakly to moderately inequilateral, with one side 1–2.5 cm wider than opposite side midway; posterior lobes directed toward the base or somewhat outward, $7.5-17 \times 3.5-8 \text{ cm}$, 2 to 2.5 times longer than wide, weakly acuminate to bluntly acute at apex, broadest midway, rarely weakly broadest at base, \pm symmetrical, the inner side broadly rounded toward base, attenuate onto posterior rib; outer side \pm straight to weakly convex toward base; midrib and major venation round-raised on lower surface, drying raised, concolorous to weakly paler than surface, occasionally weakly darker; **basal veins** 5 to 6 pairs, coalesced into a prominent posterior rib; posterior rib naked 1–1.5 cm per side; primary lateral veins 4 to 5 pairs, arising at $45^\circ-55^\circ(-65^\circ)$, weakly to moderately arcuate; secondary veins raised on lower surface, drying raised, con-

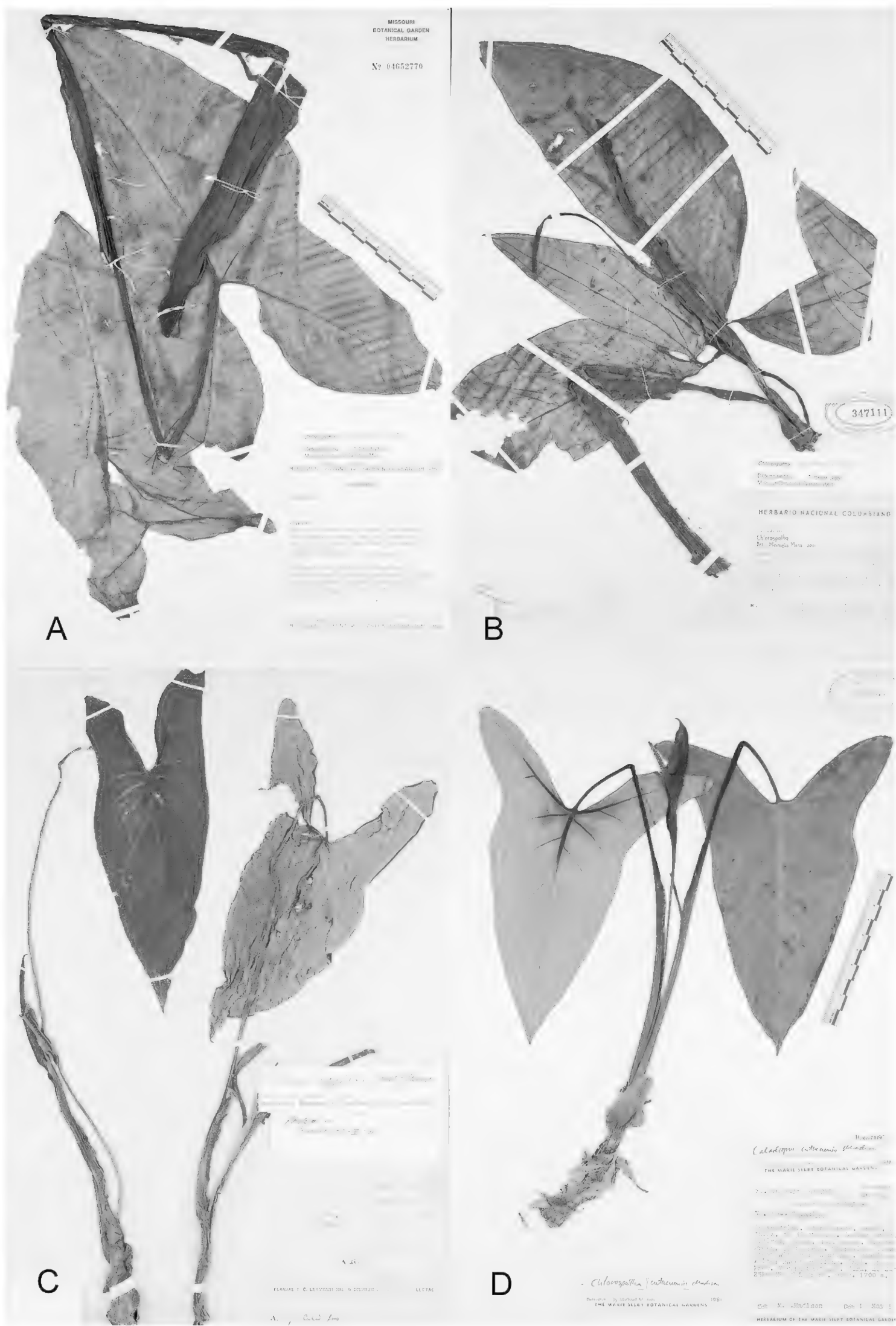


Figure 12. —A. *Chlorospatha carchiensis* Croat & L. P. Hannon, Boyle & Dalmau 1756 (MO paratype). —B. *Chlorospatha cedralensis* Croat & L. P. Hannon, the holotype Galeano et al. 2004 (COL-347111). —C. *Chlorospatha congensis* Croat & L. P. Hannon, Lehmann 389 (K holotype). —D. *Chlorospatha cutucuensis* Madison, Madison 6944 (SEL holotype).

colourous to weakly paler or weakly darker than surface; tertiary veins drying weakly to moderately prominulous on lower surface, weakly paler to weakly darker than surface; reticulate veins usually drying flat on lower surface, visible and distinct, otherwise prominulous, weakly darker than surface; collective veins 3 to 4, the innermost arising from one of the lateral veins on inner side of posterior lobe, loop-connected with all preceding lateral veins, \pm parallel to and 3–7 mm from margin. INFLORESCENCES erect, 1 to 3 per axil; peduncle held within the sheath, 27–33 cm \times 2–4 mm, drying matte to weakly glossy, dark brown to blackish brown; **spathe** erect, 10.7–11.5 cm long, cuspidate at apex; spathe tube green, 4–6 cm \times ca. 5 mm, drying weakly glossy, dark brown on outer surface; spathe blade white, ca. 5.5 cm \times ca. 5 mm, drying weakly glossy, medium yellowish tan on outer surface, marcescent, erect after anthesis; **spadix** erect, 9.5–10.8 cm long, sessile, adnate to spathe 3.6–4.4 cm at base, $\frac{3}{4}$ of the length of pistillate portion; pistillate portion pale green, 3.7–4.5 cm \times 2.5–4 mm, broadest at apex, drying medium to dark reddish brown; fertile staminate portion white, 4.5–4.8 cm \times 4–5 mm, narrowly rounded at apex, broadest near base, weakly tapering, drying dark reddish brown or weakly glossy, medium orangish brown; sterile staminate portion 4–8 \times ca. 4 mm, \pm cylindrical, drying markedly dark reddish brown; pistils weakly coherent, more laxly arranged near base (of spadix), 3 to 4 across the axis (viewed from above), 1.5–1.8 mm long; ovaries \pm cylindrical, obtusely truncate at apex, drying tan, 1–1.2 \times 1.8–2 mm; style Type 9 (Fig. 1), 0.5–0.75 \times 1.8–2 mm, comprising ca. $\frac{1}{3}$ or slightly more of the length of pistil, the margins usually \pm coherent with those of adjacent styles; **stigma** prominent, ca. 0.8 mm diam., elevated on and wider than narrowed portion of style, drying pale yellow-orange or tan; synandria ca. 1 \times 1.5–2.2 mm, coherent, \pm truncate, 3- to 4(5)-lobed, 3- to 4(5)-androus; sterile flowers 0.5–0.8 \times 0.5–2 mm, in 4 whorls, weakly coherent, occasionally deeply irregularly lobed in apical 2 whorls, otherwise 2- to 5-branched in basal 2 whorls or all whorls, the branches truncate at apex, abruptly narrowed below, a few flowers extending into apical whorl of pistils. INFRUCTESCENCE (immature) 6.5 cm \times 7 mm, drying matte, dark brown; berries not known.

Phenology. Flowering and fruiting are only known to occur in *Chlorospatha carchiensis* during the month of April.

Etymology. *Chlorospatha carchiensis* is named for Carchi Province, Ecuador, where the new species is endemic.

Discussion. *Chlorospatha carchiensis* is known only from lower montane wet forest in the vicinity of Maldonado in Carchi Province, Ecuador, on the western slopes of the Andes at 1740–1800 m elevation, and would be expected to occur in Esmeraldas Province and northward into Nariño Department, Colombia. The species is a member of *Chlorospatha* sect. *Occidentales* and is distinguished by its sagittate leaf blades that are prominently constricted on one side in the area of petiole attachment and dry matte to weakly glossy green on the upper surface and semiglossy on the lower surface, with the midrib, major, and secondary venation raised and usually concolorous to weakly paler than the surface. The posterior lobes are moderately narrow, more than 2 times longer than wide and usually broadest midway, with one lobe prominently constricted at the base. The lobes are also long, relative to the length of the anterior lobe, which is less than twice as long as the posterior lobes. *Chlorospatha carchiensis* is also distinguished by its relatively large inflorescence with a green spathe tube, white spathe blade, and green styles.

Chlorospatha carchiensis could possibly be confused with *C. narinoensis* from the western slopes of the Andes in or near the Reserva Natural Río Ñambí in Nariño Department, Colombia, at 1100–1325 m elevation. The species could ultimately prove to be sympatric, the type localities being in close proximity. *Chlorospatha carchiensis* has the petiole sheathed one half or slightly more of its length, with the sheath free-ending at the apex, and the leaf blades sagittate, with the posterior lobes significantly broader than those of *C. narinoensis*. The petiole of *C. narinoensis* is sheathed one third of its length, with the sheath decurrent at the apex, and the blades are hastate. The upper surface of the blade in *C. carchiensis* lacks the pale raphid cells observed on the blades of *C. narinoensis*, and the peduncle is significantly longer, 27–33 cm, as is the spathe, 10.7–11.5 cm. In *C. narinoensis*, the peduncle is only 12–14.5 cm long and the spathe less than 8 cm long. The spadix of the latter species is adnate to the spathe most or all of the length of the pistillate portion versus three fourths of the length in *C. carchiensis*. The style (Type 9, Fig. 1) of *C. carchiensis* comprises about one third of the length of the pistil, thus differing from that of *C. narinoensis* (Type 5, Fig. 1), which comprises about one half of the length. The sterile flowers are also different, all or most being branched in *C. carchiensis* versus subprismatic in *C. narinoensis*.

Paratype. ECUADOR. **Carchi:** vic. Maldonado, upper Río Pablo drainage, along crest of ridge to N of river,

Transect 1750-3, 1740-1780 m, 0°53'N, 78°10'W, 24 Apr.-2 May 1993, B. Boyle & L. Dalmau 1756 (CM, MO).

14. *Chlorospatha castula* (Madison) Madison, Selbyana 5(3-4): 356. 1981. Basionym: *Caladiopsis castula* Madison, Contr. Gray Herb. 208: 98. 1978. TYPE: Ecuador. Pichincha: vic. Chiriboga, 1200 m, 1975, M. Madison 4151 [non 4141, sic, Madison, 1981: 356] (holotype, SEL!; isotypes, K!, QCA!). Figure 13A-D.

Terrestrial herb, less than 1 m tall; stem possibly erect, erect 8-30 cm at apex, producing bulbils randomly along its length; bulbils ca. 1 cm long, shape of bulbils unknown; internodes short, 2-4 cm diam.; cataphylls triangular, 8-11 cm long, apex not known. LEAVES 2 to 3, erect-spreading; **petioles** 35-50 cm long, granular-puberulent at apex, entirely green toward apex, otherwise green with dark purple mottling, drying matte to weakly glossy, medium-dark to dark brown, sheathed 22.5-33.5 cm, 1/2 to 2/3 of total length; sheath decurrent at apex; free portion 3-4 mm diam. midway; **blades** sagittate-subhastate, 33-43 × 21-25.5 cm, 1.6 to 1.7 times longer than wide, acuminate at apex, broadest at base, (1.4 to)3.3 to 3.6 times wider at base than across anterior lobe (measured tip to tip across posterior lobes), frequently weakly to moderately constricted on one side in area of petiole attachment, thin, moderately bicolorous; upper surface quilted, velvety, dark green, occasionally medium green toward margins, drying matte, medium to dark greenish brown; lower surface purple-tinged medially or entirely green with midrib and major veins purplish, drying weakly glossy to semiglossy, weakly paler; anterior lobe 21-25 × 9-16 cm, 1.6 to 2.3 times longer than wide, 1.2 to 1.4 times longer than posterior lobes, broadest at or near base, ± symmetrical; posterior lobes directed somewhat outward, 16-20.5 × 4-8 cm, (2.3 to)3.4 to 4 times longer than wide, acute to weakly acuminate at apex, broadest below middle, ± symmetrical, the inner side straight to rounded toward base; midrib and major venation granular-puberulent on lower surface and ± purple-tinged, drying weakly raised and ± flattened, weakly to moderately darker than surface; midrib deeply sunken on upper surface, round-raised on lower surface; **basal veins** 6 to 8 pairs, coalesced into a prominent posterior rib; posterior rib naked 1.3-2.3 cm per side; primary lateral veins 4 to 7 pairs, arising at 40°-60°, weakly to moderately arcuate, rarely markedly arcuate, straight or irregularly ascending, quilted-sunken on upper surface, convex on lower surface; secondary veins raised on lower surface, drying ± raised, weakly to moderately darker than surface; tertiary veins raised on lower surface, drying

weakly raised, weakly to moderately darker than surface; reticulate veins drying obscure; collective veins 3, the innermost arising from one of the lowermost lateral veins on inner side of posterior lobe, loop-connected with all preceding lateral veins, parallel to and 3-4 mm from margin. INFLORESCENCES erect, 4 per axil; peduncle held within the sheath, terete, 25-37 cm × 1-2 mm, medium green, dark purple-mottled, drying matte, dark brown; **spathe** cucullate, 6.3-8.5 cm long, 2-4 cm longer than spadix, ± acute at apex, with margins in-rolled near apex; spathe tube entirely dark purple or pale green and in part narrowly dark purple at the base and along the outer margin, 3-4.3 cm × 5-7 mm, drying matte to weakly glossy, purple or purplish brown on outer surface, weakly glossy to semiglossy on inner surface and concolorous to weakly paler; spathe blade entirely cream-colored, rarely pale green at base and white at apex, 3.2-4.2 cm × 5-8 mm, drying matte, yellowish cream to pale tan, rarely cream and in part purple-tinged, with reticulate veins purplish on both surfaces, opening narrowly at anthesis, marcescent, erect after anthesis; **spadix** erect, 4.3-6.5 cm long, sessile, adnate to spathe 1.5-2.2 cm at base, most of the length of pistillate portion; pistillate portion white, 1.7-2.8 cm × 3-4 mm (dry), broadest midway, drying creamy white; fertile staminate portion cream to pale yellow-green, 1.6-2.2 cm × 3-4 mm (dry), narrowly rounded at apex, ± clavate, drying yellowish cream; sterile staminate portion purple to maroon, 1-1.6 cm × 2 mm (dry), ± cylindrical; pistils ± laxly arranged, ca. 3 across the axis (viewed from above), ca. 1.5 mm long; ovaries ± subglobose, ca. 2 mm diam., 3-carpellate, semi-unilocular, with basal placentation, drying brown; style Type 4 (Fig. 1), white, ca. 3 mm diam., thin, lacy, possibly obscurely attenuate medially, markedly broader than ovary apex, the margins ± coherent with those of adjacent styles; **stigma** yellow, ca. 0.5 mm diam. (dry), sessile, obtusely truncate, drying yellowish tan; synandria ca. 1 × 0.75-1 mm, coherent, truncate, deeply (2)3- to 4-lobed, 3- to 4-androus; sterile flowers cream-colored, with margins purple, ca. 1 mm long (or less), 2-2.5 × 1 mm diam. and ± elongated in direction of axis, weakly coherent to ± laxly arranged, fungiform, broadly and deeply concave medially, with margins irregular (probably sinuate-undulate), in ca. 5 whorls. Berries not known.

Phenology. Flowering times of *Chlorospatha castula* are not known.

Discussion. *Chlorospatha castula* is known from only two collections made in Pichincha Province, Ecuador, at 1200 m elevation on the western slopes of



Figure 13. *Chlorospatha castula* (Madison) Madison, the type collection *Madison 4151*. —A. Fertile habit in the type locality (Ecuador). —B. Leaf blade adaxial surface. —C. Close-up of petioles and inflorescences. —D. Close-up of inflorescence at anthesis. B–D, cultivated from the type at Munich Botanical Garden. A photograph by M. Madison. B–D photographs by J. Bogner.

the Andes, and would be expected to occur in the adjoining provinces. No coordinates were reported, but the species was probably collected in premontane wet forest.

Chlorospatha castula is a member of *Chlorospatha* sect. *Occidentales* and distinguished by its sagittate-subhastate leaf blades that are velvety, dark green on the upper surface and usually purple-tinged on the lower surface, and by its relatively small inflorescence with a dark purple spathe tube. Of particular note are the thin, broadly spreading style, 3 times broader than the ovary apex, and unusual concave-fungiform sterile flowers that are cream-colored medially with dark purple margins. The sterile staminate portion of the spadix comprises approximately one third of the total length, a character, which combined with the unusual sterile flowers, is found in only two other species, *C. atropurpurea* and *C. hastata*. *Chlorospatha hastata* is known only from Carchi and Esmeraldas provinces in Ecuador, and is not known to occur with *C. castula*.

Chlorospatha castula differs from *C. atropurpurea* and *C. hastata* in having the lower surface of the leaf blade only purple-tinged, whereas that of the other species is either entirely dark purple or sharply discoloured and dark purple along the major venation (see differences discussed under both species). *Chlorospatha castula* would be most easily confused with the sympatric species, *C. atropurpurea*, both of which occur in Pichincha Province, with no indication of hybridization. The ovaries of *C. castula* differ in having basal placentation, rare in *Chlorospatha*, those of *C. atropurpurea* having axile or pseudoaxile placentation and those of *C. hastata*, subaxile placentation.

Madison (1981) originally assigned *Madison et al.* 4596 to *C. castula*, but the collection better accords with *C. hastata* in all respects.

Additional specimen examined. ECUADOR. **Pichincha:** vic. Chiriboga, 1200 m, 1975, *Madison 2106* (SEL).

15. *Chlorospatha cedralensis* Croat & L. P. Hannon, sp. nov. TYPE: Colombia. Risaralda: Mpio. Pereira, El Cedral, old Salento rd., 2200–2300 m, 11 June 1989, *G. Galeano, N. Ladino, A. Castillo, P. Franco & F. Forero 2004* (holotype, COL-347111!). Figure 12B.

Herba ultra 1 m; cataphylla plus quam 26 cm longa. Petiolus 65–100 cm longus; lamina foliaris \pm 5-pedatisecta, ca. 32×36 cm, debiliter confluens inter lobos, nervis primariis lateralibus utroque 6 (in lobis lateralibus). Inflorescentiae erectae, 1 in quaque axilla; pedunculus ca. $58 \text{ cm} \times 1\text{--}2$ mm; spathe erecta ca. 9 cm longa, tubo ca.

$4.2 \text{ cm} \times 6$ mm, lamina ca. $4.7 \text{ cm} \times 7$ mm; spadix ca. 7.5 cm longus.

Terrestrial herb, more than 1 m tall; stem not known; internodes not known (all measurements made from dried material); cataphylls more than 26 cm long (total length and apex not known), drying semiglossy, dark orangish brown. LEAVES 1; **petioles** 65–100 cm long, glabrous, drying matte, dark brown, sheathed 49 cm, ca. $3/4$ of total length; sheath decurrent at apex; free portion 4–5 mm diam. midway; **blades** \pm 5-pedatisect, ca. $32 \times$ ca. 36 cm, ca. 1.1 times wider than long, drying thin, moderately bicolorous; upper surface drying matte to weakly glossy, medium-dark greenish brown, with pale, punctiform raphid cells; lower surface drying matte to weakly glossy, brownish green, moderately paler, with raphid cells visible; **medial lobe** in part not known, drying \pm acute at base and narrowly attached, 7 mm wide at point of attachment; **lateral lobes** acute to weakly acuminate at apex, \pm acute at base, occasionally weakly alate between some segments; innermost segment $20\text{--}25 \times 8\text{--}10$ cm, broadest at or below middle, 2.5 times longer than wide, moderately inequilateral, the inner side narrower; outer side 2 times wider than inner side midway; outermost segment $16\text{--}16.5 \times 5\text{--}5.5$ cm, broadest midway, 3 to 3.2 times longer than wide, moderately inequilateral, the inner side narrower; outer side to 2 times wider than inner side near base; midrib and major venation round-raised on lower surface, drying round-raised, moderately darker than surface; posterior rib naked ca. 2 cm per side; primary lateral veins (on medial lobe) not known; primary lateral veins (on lateral lobes) 6 pairs, arising at $40^\circ\text{--}45^\circ$ on innermost segment, $17^\circ\text{--}60^\circ$ on outermost segment, most acutely toward base, irregularly ascending to weakly arcuate; minor veins drying darker than lower surface; secondary veins raised on lower surface, drying raised; tertiary veins drying prominulous on lower surface; reticulate veins drying weakly prominulous on lower surface; collective veins 3, the innermost arising from lowermost lateral vein at base, loop-connected with all preceding lateral veins, conspicuously scalloped on innermost segments, 0.6–1.8 cm from margin. INFLORESCENCE erect, 1 per axil; peduncle held within the sheath, ca. $58 \text{ cm} \times 1\text{--}2$ mm, drying matte, dark brown; **spathe** erect, ca. 9 cm long (estimated; total length and apex not known), drying weakly constricted above tube; spathe tube green, $4.2 \text{ cm} \times 6$ mm, drying matte, dark brown on outer surface, matte to weakly glossy and moderately paler on inner surface, densely cream, punctiform (speckles regularly rounded, appearing as subepidermal cellular inclusions); spathe blade whitish, ca. $4.7 \text{ cm} \times 7$ mm, drying matte, medium reddish brown,

marcescent, erect after anthesis; **spadix** erect, 7.5 cm long, sessile, adnate to spathe ca. 1.8 cm at base, ca. 1/2 of the length of pistillate portion; pistillate portion ca. 3.5 cm × 3.5 mm, drying dark tan; fertile staminate portion ca. 3 cm × 3 mm, narrowly rounded at apex, ± cylindrical, weakly narrower at base, drying dark brown; sterile staminate portion 1.1 cm × 2 mm, ± cylindrical, drying medium brown; pistils weakly coherent, 3 to 4 across the axis (viewed from above), ca. 1.3 mm long; ovaries subglobose, ca. 1.5 mm diam., drying dark tan with weakly darker veins; style Type 3 (Fig. 1), 0.75–1 mm diam., drying dark purplish brown; **stigma** ca. 0.3 mm diam., sessile, obtusely truncate at apex; synandria ca. 1 × 1–1.5 mm, coherent, truncate, deeply 3- to 4-lobed, 3- to 4- (mostly 4); sterile flowers ca. 0.5 mm long, 2–3 × 0.8 mm diam., and markedly elongated in direction of axis, ± coherent or only laterally, truncate, irregularly subprismatic, in 4 whorls. Berries not known.

Phenology. Flowering in *Chlorospatha cedralensis* is only known to occur in the month of June.

Etymology. *Chlorospatha cedralensis* is named for the town of El Cedral, near the type locality in Risaralda Department.

Discussion. *Chlorospatha cedralensis* is known only from the type collection made in lower montane wet forest on the western slopes of the Cordillera Central, in the vicinity of Pereira in Risaralda Department, Colombia, at 2200–2300 m elevation, and would be expected to occur in Caldas Department to the north and in Quibdó to the south. The species is a member of *Chlorospatha* sect. *Chlorospatha* and is distinguished by its 5-pedatisect leaf blades, petiole sheathed approximately three fourths of its length, peduncle nearly as long as the petiole, and relatively small inflorescence, ca. 9 cm long.

Chlorospatha cedralensis might be confused with two species that also occur above 2000 m elevation in the Cordillera Central: *C. caldasensis* from Caldas Department to the north and *C. luteynii* from the northern portion of the mountain range in Antioquia Department (see discussions under both species). These two species have maculate, 5-lobed leaf blades that are broadly confluent between segments (confluent portion 1.5–4 cm wide), the petiole sheathed about one half of its length and the peduncle about one half as long as the petiole. *Chlorospatha cedralensis* differs in having blades that lack maculations, with segments free to the base or weakly alate between segments and acute at the base, the petiole sheathed three fourths of its length and the peduncle nearly as long as the petiole. In *C.*

caldasensis and *C. luteynii*, the lower blade surface dries semiglossy to glossy, with the midrib and major venation flattened versus matte to weakly glossy, with the midrib and major venation round-raised in *C. cedralensis*. The upper surface of the blade of *C. cedralensis* contains densely dispersed, punctiform raphid cells that do not occur in the other two species. The leaf blades of *C. caldasensis* are brown and dry brown, differing from those of *C. cedralensis*, which are green and dry greenish.

Chlorospatha cedralensis is similar to *C. croatiana* var. *enneaphylla*, both having deeply lobed leaf blades with the segments acute at the base and either occasionally alate or weakly confluent between segments, depending on the taxon; however, all Colombian collections of the latter taxon have 7- to 9-lobed blades, the petiole sheathed one half to two thirds of its length and the peduncle half as long as the petiole. In Colombia, *C. croatiana* var. *enneaphylla* is known only from below 900 m elevation in Antioquia, Boyacá, and Chocó departments, whereas *C. cedralensis* occurs only in Risaralda, at above 2000 m.

16. *Chlorospatha chocoensis* Croat & L. P. Hannon, sp. nov. TYPE: Colombia. Chocó: near Río Iró, ca. 10 km S of Istmina, less than 50 m, 5°04'30"N, 76°41'W, 13 Mar. 1984, *Croat 57402* (holotype, MO-3184311!; isotype, CHOCO!). Figure 14A, B.

Herba ca. 1 m; internodia brevia, usque ad 3 cm diam. Petiolus ca. 67.5 cm longus, vaginatus per ca. 25 cm; lamina foliaris profunde 3-loba, ca. 36 × 48 cm, lobo medio late ovato, ca. 26.5 × 20 cm, nervis primariis lateralibus utroque 5. Inflorescentiae 2 in quaque axilla; pedunculus 16–18 cm × 1–1.5 mm; spatha erecta, 7–7.5 cm longa, tubo 3.2–4 cm × ca. 6 mm, lamina 3.8–4.2 cm × ca. 5 mm; spadix 5–5.2 cm longus.

Terrestrial herb, ca. 1 m tall; stem possibly erect, to 30 cm long; internodes short, to 3 cm diam.; cataphylls (length and apex not known), drying weakly glossy, dark reddish brown, weakly fibrous. LEAVES 1, probably erect-spreading (all measurements made from dried material); **petiole** 67.5 cm long, glabrous, purple-tinged green, drying weakly glossy, dark reddish brown, sheathed ca. 25 cm, ca. 1/3 of its length; sheath free-ending at apex; free portion ca. 7 mm diam. midway, terete; **blade** deeply 3-lobed to trisect, ca. 36 × ca. 48 cm, wider than long, drying thinly coriaceous, moderately bicolorous; upper surface quilted, weakly glossy, dark green, sparsely paler maculate, drying weakly glossy to semiglossy, brownish green, with weakly paler maculations; lower surface purple-tinged, drying semiglossy to glossy, moderately paler; **medial lobe**

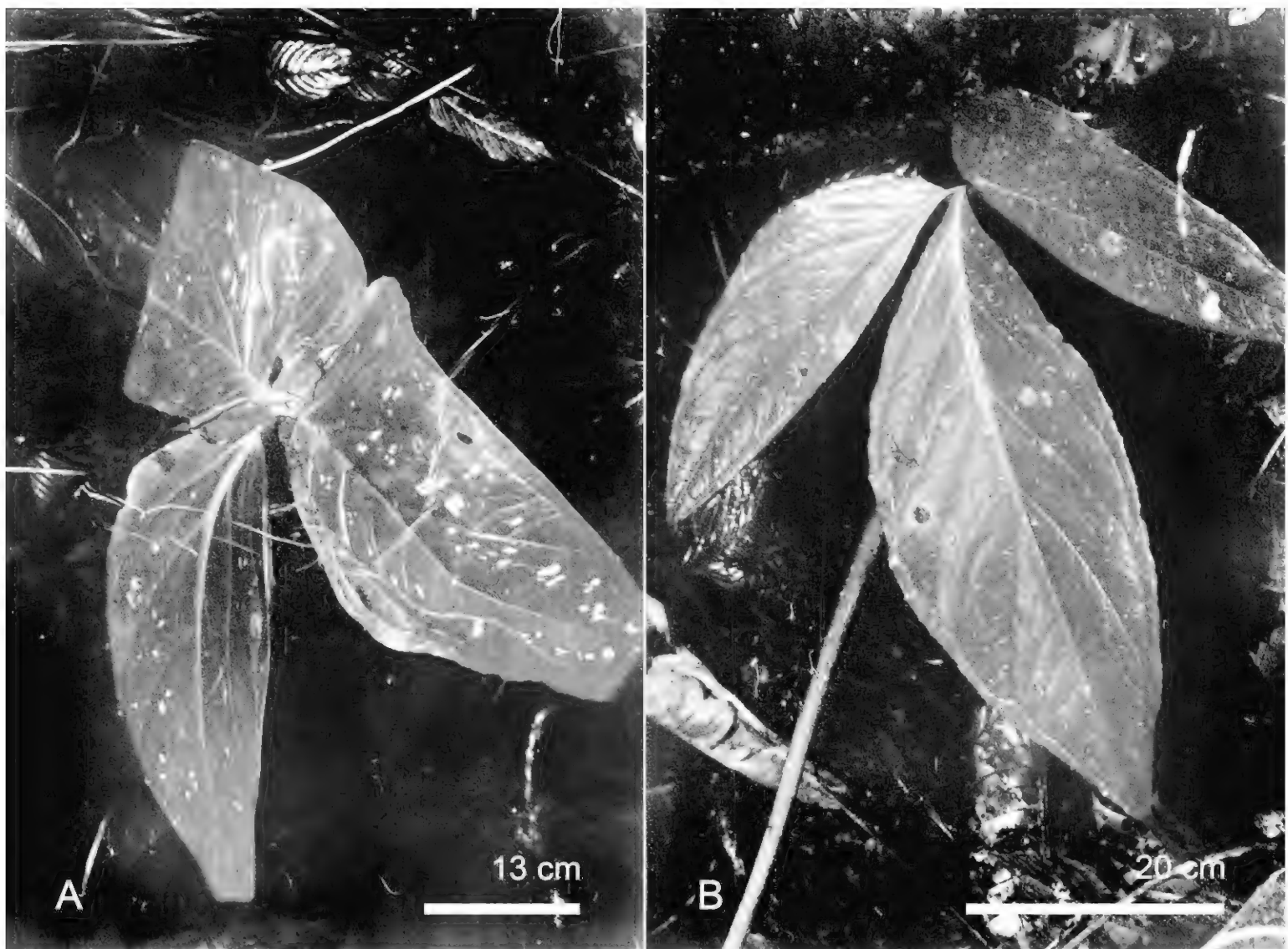


Figure 14. *Chlorospatha chocoensis* Croat & L. P. Hannon, from the type collection Croat 57402. A, B. Leaf blade adaxial surfaces.

broadly ovate, 26.5×20 cm, 1.3 times longer than wide, 1 to 1.4 times longer than lateral lobes, abruptly acuminate at apex, broadest below middle, broadly cuneate and broadly attached at base, ca. 7 cm wide at point of attachment, moderately inequilateral, one side 1.1 to 1.5 times wider than opposite side; **lateral lobes** oblique, $24\text{--}25.5 \times 12\text{--}14$ cm, 1.7 to 2 times longer than wide, broadly and weakly long-acuminate at apex, broadest midway, moderately inequilateral, the inner side narrower, \pm straight toward base and broadly confluent with medial lobe, the confluent portion 3.5–4 cm wide; outer side 1.1 to 2.2 times wider than inner side midway, broadly rounded toward base and overlapping the base of opposite lobe, decurrent onto petiole; midrib and major veins quilted-sunken on upper surface, convex on lower surface, drying \pm flattened, weakly to moderately darker than surface; posterior rib not naked; primary lateral veins (of medial lobe) 5 pairs, arising at ca. 45° , straight to weakly or moderately arcuate; primary lateral veins (of lateral lobes) 5 pairs, arising at $35^\circ\text{--}90^\circ$, most acutely toward apex, weakly to moderately arcuate; secondary veins drying weakly raised on lower surface, \pm concolorous; tertiary veins drying in part weakly prominulous and

otherwise obscure on lower surface, usually concolorous, in part weakly darker than surface; reticulate veins drying obscure; collective veins 3, the innermost arising from lowermost lateral vein at the base, loop-connected with all preceding lateral veins, prominently scalloped on lateral lobes, 0.3–2 cm from margin, weakly to moderately scalloped on medial lobe, 3–8 mm from margin. **INFLORESCENCES** erect, 2 per axil; peduncle held within the sheath, $16\text{--}18$ cm \times 1–1.5 mm, drying weakly glossy, medium to dark brown; **spathe** erect, 7–7.5 cm long, cuspidate at apex; spathe tube 3.2–4 cm \times ca. 6 mm, drying matte, medium to dark brown and paler at the margins on outer surface, matte, moderately to prominently paler on inner surface; spathe blade subcoriaceous, 3.8–4.2 cm \times ca. 5 mm, drying matte, medium to pale yellowish tan on outer surface, matte, much paler on inner surface, marcescent, erect after anthesis; **spadix** erect, 5–5.2 cm long, sessile, adnate to spathe ca. 1.6 cm at base, slightly more than 1/2 to 3/4 of the length of pistillate portion; pistillate portion 2.2–2.7 cm \times 3–5 mm, broadest toward apex, drying pale yellowish tan; fertile staminate portion 1.5–1.7 cm \times 2–2.8 mm, bluntly acute at apex, \pm cylindrical, drying medium-dark reddish brown, creamy tan at

apex; sterile staminate portion 1–1.2 cm \times 1.8–2.5 mm, broadest at base, drying cream-colored to pale tan, with numerous red speckles; pistils weakly coherent to laxly arranged, ca. 3 to 4 across the axis (viewed from above), 1.5–2 mm long; ovaries 1.5–2 mm diam., \pm cylindrical (possibly obtusely conical or subcuboidal), drying creamy white, occasionally with weakly darker veins, 3-locular; style Type 3 (Fig. 1), 1.5–2 mm diam., weakly broader than ovary apex; **stigma** disklike, 0.5–0.75 mm diam., sessile, obtusely truncate, drying brownish, darker than style; synandria ca. 1 \times 1–1.5 mm, coherent, truncate, deeply (2)3- to 5-lobed, 3- to 5-androus (mostly 4), lacking microsporangia in apical 2 whorls; sterile flowers ca. 0.5–0.75 mm long, 1.2–2.2 mm \times 0.75–1 mm diam. and \pm elongated in direction of axis, \pm laxly arranged, fungiform, broadly concave medially, with deeply sinuate margins, conspicuously and abruptly narrowed below apex, in 6 to 8 whorls. Berries not known. JUVENILE plants with petioles 23 cm \times 4 mm midway, sheathed 7.5 cm; blades maculate; **medial lobe** 15 \times 10.5 cm, broadest below middle, acuminate apex, with 3 primary lateral veins; **lateral lobes** oblique, 11.5–12 \times 4.2–4.8 cm, broadest below middle, acute to weakly acuminate at apex, broadly confluent with medial lobe, confluent portion ca. 1 cm wide, with outer sides broadly rounded at base, decurrent onto petiole, with 2 pairs primary lateral veins.

Phenology. Flowering is only known to occur in *Chlorospatha chocoensis* during the month of March.

Etymology. *Chlorospatha chocoensis* is named for Chocó Department, Colombia, where the type was collected.

Discussion. *Chlorospatha chocoensis* is known only from the type collection made near Istmina in Chocó Department, Colombia, at less than 50 m elevation, in tropical rainforest on the western slopes of the Cordillera Occidental.

The species is a member of *Chlorospatha* sect. *Chlorospatha* and distinguished by its maculate, deeply 3-lobed to trisect blades that are purple-tinged on the lower surface, as is the petiole, and by its short peduncle and unusual sterile flowers. The lower blade surface dries an unusual jade-green. The posterior rib is not naked in fully mature leaf blades of *C. chocoensis*, distinguishing it from all other taxa with divided blades.

Chlorospatha chocoensis would be most easily confused with *C. mirabilis*, which also occurs at low elevations in Chocó Department and might eventually

prove to be conspecific with this species (see discussion under *C. mirabilis*).

Chlorospatha chocoensis might also be confused with another species that occurs in Chocó, *C. maculata* (see discussion under that species). The latter species differs in having entirely green leaves (except for paler maculations), a brittle petiole, and subcoriaceous blades that are matte and not at all quilted on the upper surface, with the segments broadly concave on the upper side (observed in photographs), a condition not previously observed in the genus, possibly resulting from the considerable thickness of the blade. In *C. chocoensis*, the blades are weakly glossy on the upper surface, purple-tinged below, with the blade segments convex and quilted, and the petiole is spongy and purple-tinged. The leaf blades of *C. chocoensis* are thinner and the petiole is sheathed only one third of its length versus one half to two thirds of its length in *C. maculata*. There are more primary lateral veins on all blade segments in *C. maculata* (mature specimens), with seven to 10 pairs on the lateral lobes and six to eight pairs on the medial lobe versus five pairs on both the lateral and medial lobes in *C. chocoensis*. The primary lateral veins are aggregated in the basal one third of the lateral lobes in *C. maculata* but evenly distributed in *C. chocoensis*.

17. *Chlorospatha cogolloi* Croat & L. P. Hannon, *Aroideana* 27: 14–17. 2004. TYPE: Colombia. Antioquia: Parque Nac. Nat. Las Orquídeas, vic. Calles, on ridge to NW of La Cabaña Calles, Quebrada Honda, Parcel W, subparcels W8–W9, 1300 m, 6°29'N, 76°14'W, 11 Dec. 1992, J. Pipoly, A. Cogollo, D. Cárdenas, M. Villa, O. Alvarez & L. Velez 16992 (holotype, MO-04925669!; isotype, JAUM!). Figure 11B.

Terrestrial or hemiepiphytic herb, ca. 1 m tall (all measurements made from dried material); stem with remnants of old cataphylls persisting semi-intact at upper nodes, mostly as linear fibers, with most fibers paler; sap pink or creamy white; internodes ca. 1.5 \times 0.7–2 cm, drying matte, dark brown; cataphylls 15–30 cm long, obtuse with acumen at apex (acumen ca. 7 mm long), drying \pm fibrous, matte to weakly glossy, medium to dark reddish brown. LEAVES 1 to 3, erect-spreading; **petioles** 35–73(–95) cm long, glabrous, drying matte to weakly glossy, dark brown, sheathed 34.5–70 cm, usually 3/4 or more of its length (in mature specimens); sheath decurrent at apex; free portion 2–4 mm diam. midway, minutely many-ribbed; **blades** trisect to deeply 3-lobed (entire or with conspicuously short, broadly confluent lateral lobes in juvenile plants), 23–43(–56) \times 22–55(–65)

cm, as wide as long or weakly wider than long, drying thin to thinly coriaceous, moderately to conspicuously bicolorous; upper surface green, occasionally sparsely paler maculate, drying weakly glossy to semiglossy, dark brown to dark green; lower surface usually entirely purple, rarely entirely green with major veins purple, drying weakly glossy to semiglossy, gray-tinged green to greenish brown; **medial lobe** elliptical to narrowly long-ovate, $22\text{--}36.5(-46) \times 8\text{--}15(-18)$ cm, 2.4 to 2.7 times longer than wide, 1.2 to 1.4 times longer than lateral lobes, acuminate at apex, broadest below middle, occasionally midway, acute to cuneate toward the base and narrowly attached, 1–4 cm wide at point of attachment, weakly inequilateral to symmetrical; **lateral lobes** directed toward the apex, $(22\text{--})25\text{--}30.5(-40) \times (6\text{--})9\text{--}12(-15)$ cm, (2.2 to) 2.5 to 3.6 times longer than wide, moderately acuminate to broadly or narrowly long-acuminate at apex, broadest at or below middle, moderately to markedly inequilateral, the inner side always narrower, weakly to moderately attenuate or rarely \pm straight toward base, narrowly or not at all confluent with medial lobe, the confluent portion 1–3(–8) mm wide; outer side 1.5 to 4.7 times wider than inner side midway, moderately to broadly rounded at base, briefly attenuate onto posterior rib; midrib purple, round-raised and finely many-ribbed on lower surface, drying raised to weakly flattened, much darker than surface; posterior rib naked 1–2(–5) cm per side; primary lateral veins (on medial lobe) ca. 10 pairs (fewer in younger plants), arising at $30^\circ\text{--}45^\circ$, straight to weakly arcuate, purple, minutely many-ribbed on lower surface, drying \pm raised to weakly flattened, brown or green, moderately darker than surface; primary lateral veins (on lateral lobes) 8 to 10 pairs (fewer in younger plants), arising at $35^\circ\text{--}80^\circ$, most acutely toward apex, straight to weakly arcuate, prominently aggregated toward the base; secondary veins drying raised on lower surface, weakly to moderately darker than surface; tertiary veins drying in part weakly raised or prominulous on lower surface, otherwise flat, in part weakly to moderately darker than surface, otherwise concolorous; reticulate veins occasionally drying in part prominulous on lower surface, otherwise \pm obscure; collective veins 3, the innermost arising from one of the lowermost lateral veins at base, loop-connected with all preceding lateral veins, moderately scalloped, 2–13 mm from margin. INFLORESCENCES erect, to 4 per axil; peduncle held within the sheath, $(37.5\text{--})42.5\text{--}53$ cm \times 1–2 mm, glabrous, drying matte, dark brown to blackish brown; **spathe** erect, $(7\text{--})8.5\text{--}10.5$ cm long, cuspidate at apex; spathe tube green, $(2.7\text{--})4.3\text{--}4.5$ cm \times 5–6 mm, drying matte, dark blackish brown

on outer surface, matte and concolorous to weakly paler on inner surface; spathe blade creamy white, rarely pale green, $4.2\text{--}6$ cm \times ca. 5 mm, drying matte, blackish brown on outer surface, weakly paler on inner surface, marcescent, erect after anthesis; **spadix** erect, $(5.4\text{--})7\text{--}8$ cm long, sessile, adnate to spathe ca. 1.7 cm at base, slightly more than 1/2 of the length of pistillate portion; pistillate portion $2.3\text{--}3.3$ cm \times 3–4 mm, drying purplish brown; fertile staminate portion yellowish, ca. 3.5 cm \times 2.5–4 mm, narrowly rounded at apex, \pm cylindrical, drying medium-dark reddish to pinkish brown; sterile staminate portion $5\text{--}9 \times 1.5\text{--}2.5$ mm, weakly narrowest midway, drying dark tan to dark brown; pistils weakly coherent, ca. 4 across the axis (viewed from above), ca. 1–1.5 mm long; ovaries subglobose, 1–1.5 mm diam., drying tan; style Type 3 (Fig. 1), 1.2–1.5 mm diam., weakly broader than ovary apex, most margins \pm coherent with those of adjacent styles; **stigma** 0.3–0.5 mm diam., sessile, obtusely truncate; synandria ca. $1\text{--}1.2 \times 1\text{--}1.5$ mm, or occasionally 2×0.75 mm diam. and elongated in direction of axis in basal 4 whorls, coherent, obtusely truncate, deeply (2)3- to 4-lobed, (2)3- to 4-androus (mostly 3); sterile flowers 0.5–1 mm long, $1.5\text{--}2.5 \times 0.5\text{--}1.5$ mm diam. and \pm elongated in direction of axis, coherent, truncate, subprismatic, arranged in 4 to 5 whorls. Berries not known.

Phenology. Flowering is only known to occur in *Chlorospatha cogolloi* during the months of February, June, and December.

Discussion. *Chlorospatha cogolloi* is known only from the Parque Nacional Natural Las Orquídeas and the Nutibara–La Blanquita area near Frontino, in premontane rainforest, lower montane rainforest, or tropical wet forest on the western slopes of the Cordillera Occidental in Antioquia Department, Colombia, at 1250–1800 m elevation. The species is a member of *Chlorospatha* sect. *Chlorospatha* and is distinguished by its petiole, which is sheathed three fourths or more of its length (in mature specimens), trisect to nearly trisect leaf blades, with the lower surface usually purple but usually drying weakly gray-tinged green, and relatively small inflorescence, with the fertile staminate portion of the spadix yellowish.

Chlorospatha cogolloi would be most easily confused with *C. mirabilis*, especially juvenile or young flowering specimens, the leaf blades of both species having three to six pairs of primary lateral veins at this stage of development. However, fully mature specimens of *C. cogolloi* have eight to 10 pairs on all segments versus three to six pairs in *C.*

mirabilis. The major and secondary venation in *C. cogolloi* dries more or less raised on the lower blade surface, but flattened in *C. mirabilis*. The blades of *C. cogolloi* are thin, with the major and secondary venation drying raised on the lower surface, whereas those of *C. mirabilis* are thinly coriaceous to subcoriaceous, with the venation drying more or less flattened. The mature petiole is usually sheathed three fourths of its length in *C. cogolloi* versus one half to two thirds in *C. mirabilis*. In *C. cogolloi*, the spadix is shorter (in plants of comparable size), with the sterile staminate portion comprising only one tenth of the total length and the sterile flowers densely arranged in four or five whorls, whereas that portion comprises approximately one third of the total length in *C. mirabilis*, with the sterile flowers laxly arranged in seven to nine (to 11) whorls.

Chlorospatha cogolloi is also similar to *C. betancurii*. The latter species differs in having entirely green leaf blades with fewer primary lateral veins and the petiole sheathed about one half of its length. Its spadix is longer than seen in *C. betancurii*, with the fertile staminate portion white (see discussion under *C. betancurii*). *Luteyn 12060* (Mpio. Frontino, Nutibara district, Nutibara–La Blanquita rd., Murri region, Alto de Cuevas, 1700–1800 m, 6°45'N, 76°20'W [HUA]) is included with reservation and possibly represents another species. It is a small, fertile collection made at somewhat higher elevation, to the north of the type locality, in which the petiole is sheathed only one third of its length and the spathe is entirely pale green.

Additional specimens examined. COLOMBIA. **Antioquia:** Parque Nacional Nat. Las Orquídeas, Sector Calles, rt. bank of Río Calles, 1280–1320 m, 6°32'N, 76°19'W, 2 June 1988, *Cogollo & J. Ramírez 3160* (JAUM-016943, Fig. 11A), 1300–1490 m, 20 Feb. 1989, *Cogollo et al. 4127* (JAUM-016946, Fig. 11B); Parque Nacional Nat. Las Orquídeas, vic. Calles, right bank of Río Calles, 1350–1450 m, 6°32'N, 76°19'W, 6 Dec. 1993, *Pipoly et al. 17820* (JAUM, MO), 1250 m, 8 Dec. 1993, *Pipoly et al. 17952* (JAUM, MO).

18. *Chlorospatha congensis* Croat & L. P. Hannon, sp. nov. TYPE: Colombia. Cauca: La Conga, Popayán, along banks of Río Timbiquí, 1899, *C. Lehmann 389* (holotype, K!; isotype, K!). Figure 12C.

Herba ca. 50 cm; internodia 1–1.5 × 1–1.8 cm; cataphylla 13–16 cm longa. Petiolus 30–39 cm longus; lamina foliaris sagittata, 20–24.5 × 8–12 cm, lobis posterioribus 6–8.5 × 3–3.7 cm, nervis basalibus utroque 3, nervis primariis lateralibus utroque 5 ad 7. Inflorescentiae 3 vel 4 in quaque axilla; pedunculus 11–14 cm × ca. 2 mm; spatha erecta, 5.5–8 cm longa, tubo 2–3.7 cm × 4–5

mm, lamina 3.2–3.5 cm × 4–5 mm; spadix 4.1–6.2 cm longus.

Terrestrial herb, ca. 50 cm tall; stem with remnants of old cataphylls persisting intact along its length (all measurements made from dried material); internodes 1–1.5 × 1–1.8 cm, drying matte, dark brown; cataphylls 13–16 cm long, obtuse with acumen and inequilateral at apex, 1- to 2-ribbed abaxially, drying weakly glossy to semiglossy, medium reddish brown. LEAVES 3 to 4, erect-spreading; **petioles** 30–39 cm long, drying glabrous, matte to weakly glossy, dark reddish brown, sheathed 13–18 cm, less than 1/2 of total length; sheath decurrent at apex; free portion 2–3 mm diam. midway; **blades** sagittate, 20–24.5 × 8–12 cm, 2.1 to 2.6 times longer than wide, gradually acuminate to narrowly acuminate at apex, broadest at base, 1.1 to 1.3 times broader at base than across anterior lobe (measured tip to tip across posterior lobes), weakly or not at all constricted in area of petiole attachment, drying subcoriaceous, moderately bicolorous; upper surface drying weakly bullate, matte-subvelvety, dark reddish brown, dark purplish brown, punctiform (speckles regularly rounded, appearing as subepidermal cellular inclusions), sometimes with interrupted, dark secretory canals; lower surface drying matte to weakly glossy, occasionally obscurely and minutely dark green-spotted (10× magnification); anterior lobe 14.5–17 × 6.5–9 cm, 1.9 to 2.2 (to 2.6) times longer than wide, 2 to 2.2 times longer than posterior lobes, broadest near base, ± symmetrical; posterior lobes directed toward the base, 6–8.5 × 3–3.7 cm, 2 to 2.5 times longer than wide, bluntly acute to narrowly rounded at apex, broadest at base, ± symmetrical to weakly inequilateral, the inner side occasionally weakly narrower, ± rounded toward the base and decurrent onto petiole; outer side ± straight toward the base, occasionally weakly concave; midrib and major veins drying narrowly etched-sunken on upper surface, moderately to weakly paler than surface, prominently round-raised on lower surface, ± wrinkled and granular-puberulent; midrib drying concolorous to weakly paler or occasionally weakly darker than surface; **basal veins** 3 pairs, coalesced into a prominent posterior rib; primary lateral veins 5 to 7 pairs, arising at 30°–70°, most acutely toward apex, moderately arcuate, drying concolorous to weakly paler than lower surface; secondary veins drying etched-sunken on upper surface, prominently raised on lower surface, ± wrinkled and granular-puberulent, concolorous to weakly paler than surface; tertiary veins drying weakly sunken on upper surface, ± raised or in part prominulous on lower surface, ± wrinkled and granular-puberulent, mostly concolo-

rous, in part weakly darker than surface; reticulate veins drying weakly sunken on upper surface, in part prominulous on lower surface, otherwise visible, flat, concolorous to weakly darker than surface; collective veins 3, the innermost arising from apex of posterior rib or from a lateral vein on inner side of posterior lobe, parallel to margin to weakly scalloped, 3–6 mm from margin. INFLORESCENCES erect, 3 to 4 per axil; peduncle held within the sheath, 11–14 cm \times ca. 2 mm, drying matte, medium reddish brown; **spathe** erect, 5.5–8 cm long, gradually acuminate to cuspidate at apex, occasionally drying densely or sparsely purplish brown-speckled on both surfaces; spathe tube 2–3.7 cm \times 4–5 mm, drying matte to weakly glossy, dark reddish brown on outer surface, weakly paler on inner surface; spathe blade 3.2–3.5 cm \times 4–5 mm, drying weakly glossy, pale to dark reddish brown, marcescent, erect after anthesis; **spadix** erect, 4.1–6.2 cm long, sessile, adnate to spathe 1.8–3.2 cm at the base, the entire length of pistillate portion and 3–4 mm of sterile staminate portion; pistillate portion 1.5–2.8 cm \times 1–3 mm, drying cream-colored to pale tan; fertile staminate portion 2–2.5 cm \times 2–3 mm, narrowly rounded at apex, weakly tapering, broadest at or near base, curved weakly forward below middle, then recurved with apical 1/3 erect, drying cream to medium brownish cream; sterile staminate portion 3–9 \times 1.5–3.5 mm, broadest at base, drying medium to dark brown; pistils weakly coherent, 3 to 4 across the axis (viewed from above), ca. 2 mm long; ovary obtusely conical to \pm cylindrical, ca. 1.5 \times 1–1.5 mm, drying brownish cream with dark brown veins; style Type 10 (Fig. 1), ca. 0.5 \times ca. 1.5 mm, comprising 1/3 of the length of pistil, the margins not coherent with those of adjacent styles; **stigma** ca. 0.3 mm diam., weakly elevated on and weakly broader than narrowed portion of style, broadest at apex, depressed medially, drying yellowish amber; synandria ca. 1 \times ca. 1 mm, coherent, truncate, deeply 3- to 4-lobed; sterile flowers ca. 1 \times 1–2.5 mm, \pm elongated in direction of axis in basal whorls, less so in apical 2 whorls, coherent, truncate, irregularly subprismatic, in (3)5 to 7 whorls. INFRUCTESCENCE (immature) 4.3 cm \times 5 mm, weakly glossy, dark brown; berries not known.

Phenology. Flowering months are not known for *Chlorospatha congensis*.

Etymology. This is named for La Conga, in Cauca Department, the type locality of the new species.

Discussion. *Chlorospatha congensis* is known from only two Lehmann collections made in 1899,

presumably from premontane rainforest on the western slopes of the Cordillera Occidental in Cauca Department in southern Colombia, at 1400–1800 m elevation. The label notes report the type locality as “La Conga, Popayán, along the banks of the Río Timbiquí.” La Conga cannot be located on any map, and it is possible that it no longer exists as a place name, many place names that are 100 years old or more having been completely abandoned. However, the Río Timbiquí notation would place it on the western slopes. The first author recently found the supposed area somewhat on the dry side, with no towns or farms, but with isolated pockets of suitable habitat that could still easily support *Chlorospatha*.

Chlorospatha congensis is a member of *Chlorospatha* sect. *Occidentales* and is distinguished by its sagittate, subcoriaceous leaf blades that dry weakly bullate and velvety-matte on the upper surface, with the major venation paler than the surface. It is likely that the living plant has bullate blades as well. On the lower surface, the midrib and major and secondary venation dry prominently raised, wrinkled and paler than the surface, with the tertiary veins prominently prominulous and paler than the surface. The posterior lobes are usually more or less rounded at the apex and decurrent onto the petiole at the base. The species is also distinguished by its short peduncles and small inflorescence (less than 8 cm long), with the spadix about 6 cm long and pistillate portion short, 1.5–2.8 cm long. The spadix is unique in the genus in curving forward and then recurving, with the apex erect.

Chlorospatha congensis would be most easily confused with *C. bullata*, known only from Valle Department, Colombia, to the north (see discussion under *C. bullata*). In the latter species, the petiole is sheathed about one third of its length, and the leaf blade is thin, with the upper surface matte, not purplish brown-speckled, and the lower surface densely reticulate, with deeply sunken areoles, both in living and dried material. *Chlorospatha congensis* differs in having the petiole sheathed slightly less than one half of its length and subcoriaceous leaf blades that are velvety on the upper surface and dry brown and densely dark purplish brown-speckled, with the lower surface lacking areoles and not densely reticulate. The blades of *C. bullata* dry green, with the midrib and major venation somewhat flattened on the lower surface, differing from *C. congensis* in which these dry prominently raised. In both species, the major venation dries paler than the upper blade surface, but in *C. bullata*, the minor venation is also paler, creating a conspicuous reticulate pattern that is lacking in *C. congensis*.

The sterile flowers are irregularly lobed in *C. bullata*, often deeply so, and subprismatic in *C. congensis*.

Chlorospatha congensis could possibly be confused with *C. huilensis*, known only from the Magdalena River drainage in Huila Department, and the eastern slopes of the Andes in Putumayo Department, Colombia. *Chlorospatha huilensis* differs in having longer internodes (1.5–3.5 cm vs. 1–1.5 cm long), the petiole sheath free-ending at the apex and the leaf blades semiglossy on the upper surface and drying thin. It can be assumed from the drying texture as subcoriaceous that the upper surface of the living blades in *C. congensis* is velvety-matte. Also, the upper blade surface is densely dark purplish brown, punctiform in *C. congensis*. In *C. huilensis*, the internodes are consistently longer (1.5–3.5 cm long) and the petiole sheaths are free-ending; the internodes in *C. congensis* are short (1–1.5 cm long), and the petiole sheaths decurrent. The midrib and major veins dry concolorous on the upper surface in *C. huilensis*, with the abaxial venation less prominently raised, not at all wrinkled, and usually weakly darker than the surface. The midrib and major veins dry paler than the upper surface in *C. congensis*, with the major and secondary venation prominently raised, wrinkled, and paler on the lower surface. The posterior lobes of *C. congensis* are rounded at the apex and decurrent onto the petiole at the base, whereas those of *C. huilensis* are bluntly acute at the apex and weakly confluent at the base, with the petiole apex obscured. In the latter species, the style comprises one half of the length of the pistil in *C. huilensis* (Style Type 5, Fig. 1) and is prominently broader than the ovary apex, thus differing from that of *C. congensis*, which comprises one third of the length of the pistil and is only as broad as the ovary apex (Style Type 10, Fig. 1).

Madison (1981) assigned both collections of *Chlorospatha congensis* to *C. lehmannii*, a species also from La Conga, the type locality of both species; however, *C. congensis* differs from the latter species in significant ways (see discussion under *C. lehmannii*).

Paratype. COLOMBIA. **Cauca:** La Conga, Popayán, 1400–1800 m, *C. Lehmann* 388 (K).

19. *Chlorospatha corrugata* Bogner & Madison, *Aroideana* 8(2): 49. 1985. TYPE: Colombia. Antioquia: Vic. Sopetrán, 2 1/2 hrs. NW of Medellín, near Río Cauca & Río Aurra, [1970s], *E. Spear s.n.* (holotype, M!; isotypes, COL not seen, K!). Figure 15A–D.

Terrestrial herb, to 1 m tall; stem (possibly erect) 10 cm long or longer, with remnants of old cataphylls persisting \pm intact along its length, weakly fibrous,

the fibers pale; sap milky; internodes 1–2 \times 1.5–2.5 cm, brown, drying 1–2 cm diam., matte, dark brown; cataphylls (6–)10–23 cm long, green, drying weakly glossy to semiglossy, medium brown, with some pale, linear fibers. LEAVES 3 to 4, erect-spreading; **petioles** (13–)30–63 cm long, entirely weakly minutely puberulent to granular-puberulent or in part only toward apex, medium green, drying matte, dark brown to greenish brown, sheathed 6–18 cm, ca. (1/4 to)1/3 of total length; sheath decurrent at apex; free portion (0.25–)0.5–1 cm diam. midway; **blades** deeply 3-lobed or trisect (in some mature specimens), 26–35 \times 30–42 cm, 1.1 to 1.2 times wider than long, thinly coriaceous (dry), concolorous; upper surface prominently corrugate, weakly glossy, medium green, drying weakly glossy, medium to dark brown to brownish green or olive-green; lower surface reticulate, narrowly minutely colliculate along all veins, medium green, drying weakly glossy to semiglossy, weakly to moderately paler; **medial lobe** 16–23.5 \times 9–12 cm, \pm elliptical, broadest at or above middle, 1.7 to 2.2 times longer than wide, shorter and narrower than lateral lobes, abruptly acuminate at apex, cuneate to acute toward the base, narrowly attached, 1.4–1.8 cm wide at point of attachment (dry), weakly to moderately inequilateral, with one side to 1.8 times wider than opposite side midway; **lateral lobes** oblique or directed toward the apex, 15–30 \times (7–) 11–14.5 cm, 1.6 to 2.4 times longer than wide, abruptly acuminate to gradually acuminate at apex, broadest at or below middle, markedly inequilateral, the inner side always narrower, attenuate toward base, markedly narrowly or not at all confluent with medial lobe, the confluent portion 1–2 mm wide (moderately confluent in young plants); outer side to 7.3 times wider than inner side midway, usually broadly rounded at base and abruptly attenuate onto posterior rib or with a weakly to well-developed posterior lobe or auricle 5.5–11.5 \times 6–10 cm, narrowly rounded to rarely bluntly acute at apex, separated from lateral lobe by slender posterior rib 1.5–2.2 cm long, the inner side ca. 3–5.5 cm wide, abruptly attenuate at base, the outer side broadly rounded, weakly to prominently or not at all constricted in area of petiole attachment; all orders of venation \pm raised on lower surface, granular-puberulent to crispy-puberulent, drying \pm raised or prominently prominulous (reticulate veins), concolorous to weakly darker than surface; midrib deeply sunken on upper surface, weakly paler than surface, drying \pm concolorous, round-raised on lower surface; posterior rib naked 1.3–2 cm per side, round-raised on lower surface; posterior rib of posterior lobe (when present) naked 2–3 cm per side (including rachis), markedly curved, round-raised on

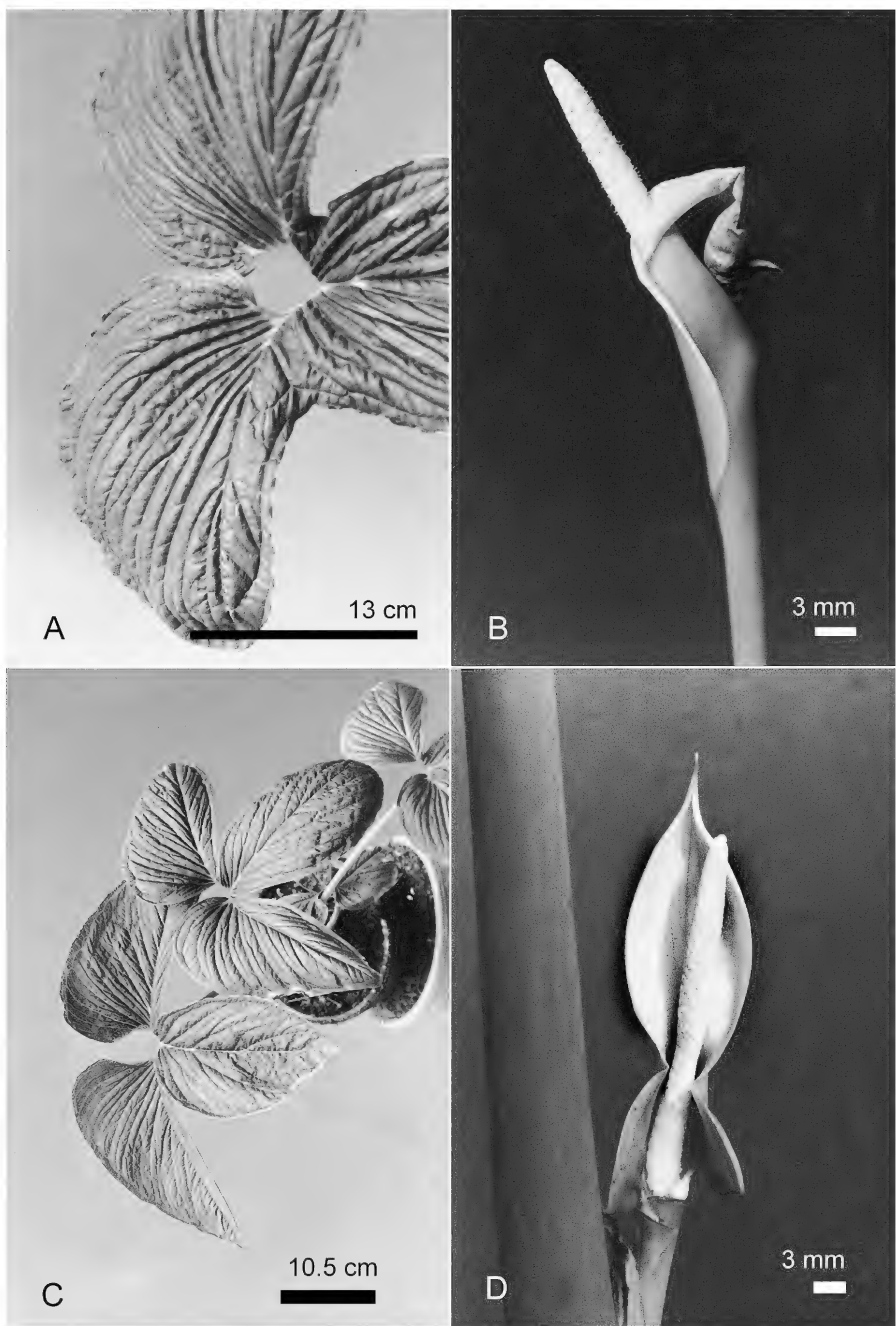


Figure 15. *Chlorospatha corrugata* Bogner & Madison, cultivar at the Munich Botanical Garden, from the type collection *Spear s.n.* —A. Close-up of the leaf blade adaxial surface. —B. Inflorescence in side view, with spathe spreading and coiled. —C. Habit of potted plant. —D. Inflorescence with spathe at anthesis (tube cut open to expose the lower pistillate portion). A–D photographs by J. Bogner.

lower surface, with 7 to 10 veins branching off, ca. 4 acroscopic, 5 basiscopic, quilted-sunken on upper surface, occasionally weakly paler than surface toward the base, drying concolorous; primary lateral veins (on medial lobe) 4 to 6 pairs, arising at 25° – 35° , straight to weakly arcuate, quilted-sunken on upper surface, weakly paler than surface, round-raised on lower surface, drying concolorous; primary lateral veins (on lateral lobes) (7)8 to 10 on outer side, arising at 40° – 45° , moderately arcuate, aggregated toward the base; secondary veins quilted-sunken on upper surface; tertiary veins in part sunken on upper surface; collective veins 3, the innermost arising from one of the lowermost lateral veins at base, loop-connected with all preceding lateral veins, weakly scalloped, 3–8 mm from margin. INFLORESCENCES erect, to 3 per axil; peduncle held within the sheath, (3–3.5)8–13 cm \times 2.5–3 mm, granular-puberulent, pale green, drying ca. 2 mm diam., matte, dark brown; **spathe** erect, 4.5–5.3 cm long, acuminate at apex, the margins in-rolled in apical 1–1.5 cm, broadly funnel-shaped at anthesis; spathe tube pale to medium green or white on both surfaces, granular-puberulent to weakly minutely puberulent on outer surface, ca. 2.3 cm long, drying 3.5–4.5 mm diam., matte to weakly glossy, dark brown to reddish brown on outer surface, weakly paler on inner surface and densely cream, punctiform (speckles regularly rounded, appearing as subepidermal cellular inclusions), most densely so toward base; spathe blade white, green, or yellowish, ca. 3 cm long, drying ca. 5 mm diam., paler than tube, opening broadly at anthesis, marcescent, reflexing after anthesis; **spadix** erect, 3.5–4.9 cm long, sessile, \pm cylindrical, adnate to spathe 6–9 mm at base, 1/2 to 2/3 of the length of pistillate portion; pistillate portion whitish, 1–1.3 cm long, drying 2.5–3 mm diam., orangish; fertile staminate portion yellowish or white, 2–2.5 cm \times 2–4 mm, bluntly acute at apex, \pm cylindrical to tapering, occasionally weakly narrowed at base, drying medium pinkish tan; sterile staminate portion creamy yellow, 0.5–1 cm \times ca. 2.5 mm, cylindrical, weakly narrower than pistillate and fertile staminate portions, drying yellowish; pistils weakly coherent, ca. 4 across the axis (viewed from above), 1–1.5 mm long; ovaries 1.5–1.9 mm diam., subglobose, with axile placentation, drying pale yellowish; ovules hemianatropous; style Type 4 (Fig. 1) (possibly Type 6, Fig. 1), whitish, 1–1.5 mm diam., moderately broader than ovary apex, the margins weakly coherent with those of adjacent styles; **stigma** disklike, lemon-yellow, 0.7–0.8 mm diam., sessile or apparently so, weakly depressed medially, drying medium reddish brown; synandria ca. 1.3 \times 1.8–2 mm, coherent, truncate, irregularly 3- to 4-lobed, 3- to 4-androus,

with a few at the apex lacking microsporangia; pollen in tetrahedral tetrads, ca. 42 microns diam., obscurely punctate; sterile flowers ca. 1 mm long, 1.5–3 \times 0.8–1.3 mm and \pm elongated in direction of axis, coherent, truncate, irregularly subprismatic, arranged in 3 to 6 whorls. INFRUCTESCENCE 3.5 \times 1 cm, drying dark brown, almost black, weakly minutely puberulent on outer surface; berries not known. CHROMOSOMES $2n = 26$ (Mayo et al., 1999).

Phenology. Flowering is only known to occur in *Chlorospatha corrugata* in March, April, and July, with fruiting recorded for the month of July.

Discussion. *Chlorospatha corrugata* is known only from Antioquia Department, Colombia, at 890–1350 m elevation, in premontane rainforest or possibly tropical wet forest, and is the only member of *Chlorospatha* sect. *Occidentales* with divided leaf blades. No other species occurs on the western slopes of both the Cordillera Central and Cordillera Occidental; however, the type locality in the vicinity of Sopetrán, near the Río Cauca in the Cordillera Central, is possibly in error. The type is the only collection from this area and the information regarding the collection was obtained only recently, by way of personal communication with Mrs. Elaine Spear, the collector of the type. However, it is unlikely that these apparently widely separated collections represent more than one species. They appear to accord in all respects except in the size of the leaf blades and the presence of a posterior lobe in one collection from the Cordillera Occidental (*Callejas et al.* 6706), which can be reasonably attributed to maturity or age, and in the color of the synandria, which are yellowish in the type and white in the other collections.

Chlorospatha corrugata is distinguished by its deeply 3-lobed to trisect, concolorous, corrugate, medium green leaf blades that are densely reticulate on the lower surface, with all orders of venation raised and puberulent to granular-puberulent. The lateral lobes are distinctive, being unusually long and broad, usually longer and wider than the medial lobe, and markedly inequilateral. The species is also distinguished by its short peduncle (to 13 cm long) and small inflorescence, less than 6 cm long, with the spathe blade reflexing after anthesis, a condition observed in only two other species of *Chlorospatha*.

Chlorospatha corrugata could not be easily confused with any other species. Only *C. risaraldensis* shares its unusual blade shape and will be considered under that species. *Chlorospatha risaraldensis* is a member of *Chlorospatha* sect. *Chlorospatha* and occurs only on the western slopes in Risaralda Department, Colombia, to the south (see discussion for *C. risaraldensis*).

Additional specimens examined. COLOMBIA. **Antioquia:** Mpio. Frontino, La Blanquita District, Region Murri, betw. Nutibara & La Blanquita, 14.5 km W of Nutibara, 15–16 km from Alto de Cuevas–La Blanquita, 890–900 m, *Callejas et al.* 6706 (MO, HUA); Mpio. Urrao, Parque Nac. Nat. Las Orquídeas, Sector Calles, Quebrada “La Agudelo,” 1300–1350 m, *J. Ramírez et al.* 4102 (MO).

20. *Chlorospatha croatiana* Grayum, Ann. Missouri Bot. Gard. 73: 464. 1986. TYPE: Panama. Coclé: N slope & summit of Cerro Pilón, 900–1173 m, 13 Mar. 1973, *Croat* 22932 (holotype, MO-3272450!; isotypes, B not seen, K!, PMA not seen, US!). Figures 16A–D, 17A–D.

Terrestrial herb, rarely hemiepiphytic, 0.5–2 m tall; stem decumbent or erect, in part subterranean, erect 5–50(–100) cm, occasionally producing bulbils randomly along its length, remnants of old cataphylls persisting as pale to medium brown fibers along its length; bulbils solitary, 0.5–2.2 cm \times 3–12 mm, covered in brown fibers; sap milky or transparent; internodes 0.3–2(–3.3) \times 0.8–4 cm, medium to dark brown, weakly scurfy, rarely with epidermis peeling and curling back at base of stem (*Croat* 83606), drying matte, dark brown; cataphylls lanceolate, becoming fibrous, 2 to 4 per leaf, 9–23(–25) cm long, acute or obtuse and inequilateral with acumen at apex (acumen to 1 cm long), obtusely 1-ribbed in apical 1/2 and longitudinal veins prominulous abaxially, weakly glossy, medium purplish, broadly dark purple along margins and abaxial rib, densely purple-mottled in narrow transverse bands, glossy and much paler on inner surface, drying matte to weakly glossy, dark reddish brown. LEAVES 1 to 4, erect to erect-spreading; **petioles** 31–78(–100) cm long, spongy or fleshy, glabrous, matte to semiglossy, green, purple, purplish or purplish brown, or green and purplish toward the base or entirely or in part purple-, purple-brown- or darker green-mottled, usually in narrow transverse bands, rarely gray-mottled, drying matte to weakly glossy, medium-dark to dark reddish brown, occasionally blackish, weakly fibrous, sheathed (14–) 18–50 cm, 1/4 to 2/3 of total length; sheath decurrent at apex; free portion 3–8 mm diam. midway, terete or obtusely flattened near apex adaxially, with margins weakly sharp, occasionally with obtuse medial rib; **blades** held horizontally to drooping, 3- to 5-lobed to \pm pedatisect and usually prominently auriculate, or 5- to 9-lobed with auricles lacking, (20–)24–44(–56) \times 20–60 cm, 1.1 to 1.5 times wider than long, occasionally as long as or weakly longer than wide, thin to thinly coriaceous, rarely subcoriaceous, conspicuously bicolorous, occasionally moderately so, the margins occasionally weakly broadly sinuate; upper surface \pm flat to broadly quilted, rarely weakly

corrugate, velvety, matte, weakly glossy or semiglossy, dark green, rarely gray-green, occasionally sparsely white or pale yellow maculate (maculations small), drying matte or weakly glossy to semiglossy, dark green to olive-green or brownish green, rarely greenish brown; lower surface matte to weakly glossy, drying weakly glossy to semiglossy, occasionally glossy, occasionally yellow-green, grayish, or with a silvery sheen, moderately to conspicuously paler; all segments \pm broadly to narrowly elliptical, ovate or obovate, rarely \pm lanceolate, weakly, gradually, or abruptly acuminate at apex, rarely acute, moderately to markedly narrowed toward and moderately to markedly narrowly attached at base, narrowly to moderately confluent between segments, the confluent portion (0.05–)0.1–2.5(–3) cm wide; **medial lobe** 19–36(–44) \times 7–21 cm, (0.3–)1–5(–7) cm wide at point of attachment, (1.5 to)1.9 to 3.6(to 4.8) times longer than wide, occasionally equal in length to or weakly shorter than innermost lateral segment, acute, attenuate or occasionally cuneate at base, weakly to moderately inequilateral, with one side 1.1 to 1.5(to 2) times wider than opposite side midway; **lateral lobes** 9–33 \times (1.5–) 2–15.5(–21) cm, (1.5 to)1.9 to 4(to 5) times longer than wide, progressively shorter and weakly to moderately narrower toward outermost segments, rarely with innermost segment weakly broader than medial segment, weakly progressively inequilateral toward outermost segments, rarely markedly so, the inner side always narrower, usually attenuate at base, occasionally acute; outer side (1.2 to)1.6 to 2.6(to 4) times wider than inner side midway; outermost segment rounded, acute or truncate at base on posterior side, with or without a weakly to well-developed auricle 7–12 \times 2–4.5 cm, acute to narrowly or bluntly rounded at apex, with weakly to well-developed midrib 2.5–8.5 cm long, with 3 to 10 veins branching off, 2 to 6 acroscopic, 1 to 4 basisopic, with inner side 0.5–2 cm wide midway, the outer side 1.5–2.5 cm wide midway and weakly to prominently constricted at base; all orders of venation glabrous on lower surface; midrib and major venation obtusely to moderately or deeply sunken on upper surface, concolorous to occasionally weakly darker than surface, convex or round-raised to acutely raised on lower surface, concolorous to moderately darker than surface, drying weakly to moderately raised, rarely \pm flattened, concolorous or weakly paler to conspicuously darker than surface; posterior rib naked 2.5–5.5(–8) cm per side, frequently markedly curved; primary lateral veins (on all segments) 2 to 7(8) pairs, arising at 15°–60°, most acutely toward apex, weakly to moderately arcuate, occasionally \pm straight; secondary veins flat or obtusely sunken on upper surface, rarely narrowly



Figure 16. *Chlorospatha croatianae* Grayum subsp. *croatiana*. —A. Habit. —B. Fertile plant. —C. Close-up of three inflorescences, one at anthesis. —D. Cluster of inflorescences. A, D from *Croat 74821* (MO). B, C from cultivated plants at MO from *Croat 67109*.

sunken, weakly to conspicuously raised on lower surface, concolorous to weakly darker than surface, drying weakly to moderately raised, prominulous or in part weakly raised and otherwise flat, concolorous to moderately darker than surface; tertiary veins flat or occasionally sunken on upper surface, entirely weakly to prominently raised, or flat and visibly distinct, or in part raised and otherwise visibly distinct on lower surface, concolorous to weakly darker than surface, drying weakly to moderately raised, prominulous, flat and visibly distinct or obscure, concolorous to moderately darker than surface; reticulate veins flat, rarely in part obtusely sunken on upper surface, flat and visibly distinct or obscure on lower surface, rarely weakly raised, drying obscure to occasionally visibly distinct or in part prominulous and otherwise flat, concolorous to weakly darker than surface, rarely in part moderately darker; collective veins 2 to 4, arising from lowermost lateral vein at the base, occasionally from the base or lateral vein near the base, loop-connected with all preceding lateral veins, markedly scalloped and remote from margin, 0.3–3 cm from margin, occasionally \pm parallel to margin. INFLORESCENCES erect, 3 to 8 per axil, emitting a sweet fragrance at anthesis; inflorescence cataphyll 2-ribbed abaxially; peduncle held within the sheath, 11–50 cm \times 2–5 mm (1–4 mm diam. dry), terete or obtusely cylindroid and thicker than broad, glabrous, entirely purple or matte, medium green to yellow-green and darker green- or purple-mottled in narrow transverse bands, most densely so toward base, drying matte to weakly glossy, medium to dark brown or blackish; **spathe** moderately to markedly cucullate, (4.6–)6–9.5(–10) \times ca. 0.5–1.2 cm (to 1.8 cm diam. at anthesis), cuspidate at apex, opening \pm broadly 1/2 to 3/4 of its length at anthesis, the margins directed forward; spathe tube matte to weakly glossy, white, cream, or pale to medium green or yellow-green on outer surface, glossy, green or purplish on inner surface, (1.8–)2.3–6 cm long, drying matte to weakly glossy, medium to dark greenish brown or brown on outer surface, matte to weakly glossy on inner surface, weakly to moderately paler; spathe blade weakly glossy to semiglossy, white, cream, pale green, or pale yellow-green, narrowly glossy and cream along margins on outer surface, matte on inner surface, (2.6–)3.5–6 cm long, occasionally obtusely 1-ribbed abaxially, drying matte, tan to medium brown on outer surface, matte on inner surface, rarely semiglossy, marcescent, erect after anthesis; **spadix** erect or curving weakly forward, 3.9–8 cm long, frequently markedly shorter than spathe (to 4 cm shorter), sessile or stipitate 2–6 mm, adnate to spathe 0.7–2(–3) cm at base, 1/5 to 3/5 of the length of pistillate portion, rarely to 3/4 or not at

all, the axis pale green; pistillate portion white or yellow, (1.2–)1.5–3.7 cm \times 3–6 mm, drying 2–5 mm diam., medium brown to dark purplish brown; fertile staminate portion white, cream, yellowish, or greenish cream, purple (*Hammel 2571*) or yellow (*Callejas et al. 4570*), (1.5–)1.7–3.7 cm \times 3–7 mm, narrowly rounded at apex, \pm cylindrical to weakly tapering, weakly broadest at base or toward middle, drying medium to dark purplish brown, occasionally yellowish tan; sterile staminate portion cream or pink (*Dressler 4884*), (0.1–)0.3–1.5(–1.7) cm \times 3–8 mm, \pm cylindrical or broadest at base, frequently with axis naked 1–4 mm at base, drying brownish cream, pale to medium tan or dark brown, with orange chromoplasts; pistils weakly coherent to \pm laxly arranged, 3 to 6 across the axis (viewed from above), 1.5–2 mm long; ovaries \pm conical, cylindrical or ovoid, occasionally subglobose on drying, white or lavender-tinged white, dark purple-tinged at base (*Croat 74799*), 1.5–2 mm diam., drying white, cream or pale tan, 2- to 3-locular (mostly 3), with axile or subaxile placentation; ovules 7 to 10 per locule, large, hemianatropous, biseriate or disorganized and uniseriate; funicle shorter or longer than ovule; style Type 3 (Fig. 1), 0.2–0.5 \times 1–2 mm, as broad as or weakly broader than ovary apex, the margins usually not coherent with those of adjacent styles; **stigma** white or pale green, 0.5–0.8 mm diam., sessile or apparently so, \pm cylindrical or weakly broadest at apex, coronate and concave medially; synandria 1–1.2 \times 1.5–2.2 mm, coherent, truncate, deeply (2)3- to 5-lobed, (2)3- to 5-androus (mostly 3 to 4); pollen (pictured in Grayum, 1984) in planar tetrads, inaperturate, coarsely foveolate or reticulate, the individual grains 24–31 μ m diam. (mean, 27 μ m), starchless, binucleate; sterile flowers in 1 to 6 whorls (rarely with none at all), 1–1.8 \times 1–2 mm, or 1 \times 1.5–2 mm diam. and \pm elongated in direction of axis, \pm coherent to laxly arranged, subprismatic, irregularly lobed or fungiform (like toadstools) and broadly concave medially, rarely 2- to 4-branched in basal 1 to 2 whorls, the branches \pm clavate and obtusely truncate at apex. INFRUCTIONES (4–)5.5–9 \times 1–1.5 cm; berries white, 3–5 mm diam.; seeds white, 13 to 25 per berry, 1–1.5 mm long, ovoid, longitudinally striate, minutely brown-strophiolate.

Discussion. *Chlorospatha croatiana* is widely distributed in Panama, with a few sterile collections having been made on the Atlantic slopes in Costa Rica, and occurs southward into northwestern Colombia.

Chlorospatha croatiana is distinguished by its frequently large size (1–2 m tall) with the stem erect, occasionally to as much as 1 m, and the internodes relatively short, rarely more than 2 cm long. The species

is also distinguished by its thin to thinly coriaceous, rarely subcoriaceous, 3- to 9-pedatifid leaf blades that are narrowly to moderately confluent between segments and usually conspicuously bicolorous, with the lower surface matte. The innermost collective vein is conspicuously scalloped and remote from the margin, occasionally to almost 3 cm from the margin. The spathe is short (relative to plant size), rarely as much as 10 cm long, and the spadix is cylindrical and frequently much shorter than the spathe (to 4 cm shorter), which is usually prominently cucullate.

Chlorospatha croatiana, as defined by Grayum (1986), consists of one subspecies and one variety, with the typical subspecies restricted to Panama and Costa Rica and variety *enneaphylla* restricted to the western slopes of the Cordillera Oriental and eastern slopes of the Cordillera Central in Colombia. The typical subspecies has leaf blades with three to five lobes, with the posterior side of the outermost lobes more or less rounded at the base or prominently, broadly auriculate. In contrast, variety *enneaphylla* typically has seven to nine lobes that are narrower, with the outermost lobes acute at the base and lacking prominent auricles. Recent studies in Panama have shown that variety *enneaphylla* occurs in the same localities as subspecies *croatiana*, precluding the possibility that it is a subspecies, not being separated geographically, elevationally, or ecologically. Two recent collections were made in Chocó Department, Colombia, on the Panamanian border, near Acandí. Therefore, the epiphet *enneaphylla*, previously known as a subspecies, should now be considered only a variety of *C. croatiana*. Sterile collections of *Chlorospatha* var. *enneaphylla* (Grayum) Croat & L. P. Hannon with 7-lobed blades were made in Panama, in Coclé and Veraguas provinces. As well as having 7- to 9-lobed blades, variety *enneaphylla* may have as few as five lobes, with the segments acute, narrowly attached, and narrowly confluent between segments or nearly free at the base versus consistently broadly attached (not acute) and more broadly confluent at the base in the species. *Chlorospatha croatiana* var. *enneaphylla* has only two to four pairs of primary lateral veins arising at 15°–35° versus five to seven (eight) pairs arising at 35°–60° in the species. The distinction between the two subspecies is based less on the quantity of lobes on each blade and more on the nature of the lobes. Since the degree to which the blades of aroid taxa are compound or deeply lobed is highly variable, through both age and geographical distribution, it is not surprising that both of these subspecies are more variable in the number of lobes than was initially assumed. However, the nature of the lobes, especially the shape, venation, and degree to

which auricles develop on the outermost segments, is uniform and consistently different in the two subspecies of *C. croatiana*.

KEY TO THE SUBSPECIES AND VARIETIES OF *CHLOROSPATHA CROATIANA*

- 1a. Terrestrial, 1–2 m tall; internodes 3–10 mm long; leaf blade 3- to 5-lobed to \pm pedatisect; segments broad, broadly attached at the base, the outermost rounded or prominently auriculate on the posterior side at the base; primary lateral veins 5 to 7(8) pairs, arising at 35°–60°; petiole sheathed 1/4 to 1/2 of its length; posterior rib naked 2.5–4(–5.5) cm per side; pistils weakly coherent, 5 to 6 across the axis (viewed from above); Costa Rica to Panama, 200–1173(–1400) m *C. croatiana* Grayum subsp. *croatiana*
- 1b. Terrestrial or hemiepiphytic, ca. 1 m tall or less; internodes 0.8–3.3 cm long; leaf blade 5- to 9-lobed to \pm pedatisect; segments narrow, narrowly attached and \pm acute at the base, the outermost not prominently auriculate on the posterior side; primary lateral veins 2 to 4 pairs, arising at 15°–35°; petiole sheathed 1/2 to 2/3 of its length; posterior rib naked 4–8 cm per side; pistils \pm laxly arranged, 3 to 4 across the axis (viewed from above); Colombia and Panama, 150–1000(–1135) m *C. croatiana* var. *enneaphylla* (Grayum) Croat & L. P. Hannon

20a. *Chlorospatha croatiana* Grayum subsp. *croatiana*. Figure 16A–D.

Terrestrial herb, 1–2 m tall; sap milky; internodes 3–10 mm \times to 4 cm, drying 0.6–2.5 mm diam.; **petioles** 31–100 cm long, sheathed 1/4 to 1/2 of total length; **blades** 3- to 5-lobed to \pm pedatisect, usually prominently auriculate; upper surface rarely pale yellow maculate; all segments broadly elliptical, ovate or obovate, gradually or abruptly acuminate at apex, moderately confluent between segments, the confluent portion 1–2.5(–3) cm wide; outermost segment \pm rounded or auriculate at the base on posterior side; posterior rib naked 2.5–4(–5.5) cm per side; primary lateral veins 5 to 7(8) pairs, arising at 35°–60°; tertiary veins drying weakly to moderately raised or prominent on lower surface; reticulate veins drying occasionally visibly distinct or in part prominent on lower surface. INFLORESCENCES 3 to 8 per axil; **spathe** (4.6–)6–9.5(–10) cm long; **spadix** 3.9–8 cm long, sessile or stipitate; fertile staminate portion white, cream, purple, or yellowish to greenish cream; sterile staminate portion 0.3–1.5(–1.7) cm long; pistils weakly coherent, 5 to 6 across the axis (viewed from above); sterile flowers subprismatic, irregularly lobed, fungiform or 2- to 4-branched.

Phenology. Flowering occurs in *Chlorospatha croatiana* subsp. *croatiana* in all months except January and November, with fruiting collections

having been made in February, March, April, May, June, August, and October. Inflorescences emerge from the petiole sheath in quick succession, each reaching anthesis approximately one to three days after anthesis of the preceding inflorescence. *Dressler 4884* reports the spathe as being full of small beetles.

Discussion. *Chlorospatha croatianana* subsp. *croatiana* is widespread in Panama, occurring on both sides of the Continental Divide and in all provinces except Chiriquí, Herrera, and Los Santos, at 200–1400 m elevation, usually at 700–1000 m, and is found on steep, wet slopes along creeks, rivers, roads, and trails, in premontane rainforest, lower montane rainforest, tropical wet forest, premontane wet forest, and lower montane wet forest. The dry conditions existing in the provinces of Herrera and Los Santos would not sustain subspecies *croatiana*, but it undoubtedly occurs in Chiriquí Province, as does variety *enneaphylla*, and would be expected to occur in Colombia, some collections from Darién and San Blas provinces having been made near that border. Four collections were made on the Atlantic slope in Costa Rica, at 200–750 m elevation, in tropical wet forest, premontane rainforest (Monteverde Reserve), and in transitional forest from tropical wet forest to premontane wet forest. These collections represent the northern limit of the species as well as the genus, although it is likely that the species extends into southeastern Nicaragua. Unfortunately, all Costa Rican collections are sterile, but these accord well with subspecies *croatiana*.

Chlorospatha croatianana subsp. *croatiana* is a member of *Chlorospatha* sect. *Chlorospatha* and is distinguished by its terrestrial habit, frequently large size (1–2 m tall, with the stem to 4 cm diam. and erect to 1 m), and short, brown internodes (3–10 mm long), with the cataphylls retained as pale to medium brown fibers. The leaf blade is 3- to 5-lobed and usually prominently auriculate. As Grayum (1986) noted, *C. croatianana* subsp. *croatiana* is variable, occasionally highly so in many respects, and is the most variable taxon in the genus. Most of the variation is observable within a small area around the sawmill near El Copé in Coclé Province, where numerous collections have been made. The petiole is consistently terete in the free portion, but can be entirely green, purple or purplish brown, or mottled with purple, green, purplish brown, or gray, and can be sheathed one fourth to one half of its length, with the peduncles accordingly long or short. The upper surface of the leaf blade can be flat or quilted, velvety to matte, or weakly glossy to semiglossy. *Croat 74821* from this area represents several extremes, having all segments almost as wide as long and corrugate on the

upper surface, with seven to eight pairs of primary lateral veins, all but the reticulate venation quilted-sunken on the upper surface and all venation raised on the lower surface. Considerable variation occurs also in the inflorescence. The color of the spathe is somewhat variable on the outer surface and the inner surface of the tube can be green or purple. Remarkable variation occurs in the sterile flowers, which can be coherent to laxly arranged, and, although subprismatic in the type and other collections, are frequently irregularly lobed and occasionally fungiform (like toadstools) or branched.

Chlorospatha croatianana subsp. *croatiana* would be most easily confused with *C. luteynii*, also with 5-lobed blades, known only from the northern portion of the Cordillera Central in Antioquia Department, Colombia, at 2440–2800 m elevation. *Chlorospatha luteynii* differs in having prominently maculate leaf blades. Weak maculations were observed on only one blade of a sterile collection from Costa Rica, of what is presumably *C. croatianana* subsp. *croatiana*, with the other blades (on the same plant) lacking maculations. The petiole of *C. luteynii* dries with the epidermis partially separated intact and semi-transparent, differing from that of *C. croatianana* subsp. *croatiana*, which usually dries somewhat fibrous, with the epidermis not separated. The spathe of *C. croatianana* subsp. *croatiana* is 6–9.5(–10) cm long versus 9–12 cm long in *C. luteynii*. The most noteworthy differences lie in the inflorescence, particularly the structure of the spadix. The spadix of *C. luteynii* is adnate to the spathe most of the length of the pistillate portion and is significantly longer, 8.5–9.5 cm long versus 3.9–8 cm long in *C. croatianana* subsp. *croatiana* in which the spadix is adnate one fifth to three fifths of the length of the pistillate portion (rarely to three fourths). The fertile staminate portion is cylindrical to weakly tapering in *C. croatianana* subsp. *croatiana*, narrowly rounded at the apex, and approximately as long as or shorter than the pistillate portion, differing from that of *C. luteynii*, which is prominently tapering, acute at the apex and more than 2 cm longer than the pistillate portion, occasionally almost twice as long. In *C. croatianana* subsp. *croatiana*, the sterile flowers are usually laxly arranged, not elongated in the direction of the axis and only occasionally subprismatic, differing from those of *C. luteynii*, which are densely arranged and consistently subprismatic and prominently elongated in the direction of the axis. The innermost collective vein is conspicuously scalloped and remote from the margin in *C. croatianana* subsp. *croatiana*, and only moderately scalloped and not markedly remote from the margin in *C. luteynii*.

Chlorospatha croatiana subsp. *croatiana* could possibly be confused with another large, 5-lobed species, *C. caldasensis*, known only from the western slopes of the Cordillera Central in Caldas Department, Colombia, at 2250 m elevation (see discussion under *C. caldasensis*).

Additional specimens examined. COSTA RICA. **Heredia:** Atlantic slope of Volcán Barva, forest betw. Río Peje & Río Sardinalito, 700–750 m, *Grayum* 6657 (MO). **Limón:** Cordillera de Talamanca, ridge separating Quebrada Cañabral from Río Barbilla, slope down to latter, 200–400 m, *Grayum et al.* 8742 (CR, MO); vic. Guápilles, 300–500 m, *Standley* 37356 (US). **Puntarenas:** Monteverde Res., Atlantic slope, drainage of Río Peñas Blancas, 750 m, *Hammel et al.* 15383 (INB, MO). PANAMA. **Bocas del Toro:** along Fortuna–Chiriquí Grande rd., 8.5 mi. N of bridge over Fortuna Lake, 4.3 mi. N of Continental Divide, 590 m, *Croat & Grayum* 60208 (K, MO, NY, US); 1.1 mi. W of Fortuna–Chiriquí Grande rd., near Continental Divide, 8°44'N, 82°17'W, 11 Mar. 1985, *Croat & Grayum* 60343 (MO); along rd. betw. Fortuna Dam & Chiriquí Grande, along gravel rd. departing main hwy. near Continental Divide, 4.5 mi. N of bridge over Fortuna Dam, 1170 m, *Croat* 66627 (MO); Chiriquí Grande–Fortuna, above waterfall, 1.6 mi. N of Continental Divide, 770–790 m, *Croat & Zhu* 76465 (MO). **Coclé:** vic. Alto Calvario, near sawmill above El Copé, 4.5 mi. N of El Copé, 2.5 mi. N of Escuela Barrigón, 580–740 m, *Croat* 67528 (MO), 710–800 m, 68753 (MO), 680–770 m, *Croat* 74821 (B, F, K, MEXU, MO, US); N of El Valle de Antón, forest betw. fork in rd. near Finca Mandarinas, along rd. to Finca Furlong, 785 m, *Croat* 67109 (F, MO); El Valle de Antón region, at La Mesa, 3.2 mi. above El Valle, 0.1 km E of Finca Macarenita, 775 m, *Croat* 74799 (M, MO, PMA), back side of Cerro Gaital, *Croat* 83606 (MO); vic. Alto Calvario & near sawmill above El Copé, betw. La Junta & Limón, 5 hr. walk N of Alto Calvario, 800–1000 m, *Folsom* 5870 (MO), La Pineda–El Copé rd., via Piedras Gordas, 914 m, *Hammel* 2571, 3528 (MO), *Hammel & Kress* 11329 (DUKE), 750–800 m, *Knapp & Dressler* 3471 (MO), 793 m, *Kress et al.* 83–1599 (DUKE); La Mesa area, along trail toward Los Llanos & border betw. Coclé & Panamá Prov., N of El Valle de Antón, 800–850 m, *Luteyn* 3155 (DUKE); near sawmill, *Folsom* 2663 (MO); **Colón:** headwaters of Río Piedras, ca. 11 km SW of Cerro Braja, 600–700 m, *Sytsma et al.* 4244 (MO). **Darién:** middle slopes on W side of Cerro Pirre, 800–1050 m, *Croat* 68943 (M, MO); Cerro Pirre, around camp at summit of Pirre, near triangulation marker, 1400 m, *Folsom* 4340 (MO); Cerro Sapo, ca. 5 km S of Garachiné, along ridge at N approach to hill, 800–1000 m, *Hammel et al.* 14867 (MO). **Panamá:** Cerro Campana, W of Canal Zone, *Bartlett & Lasser* 16938 (MICH, MO, UC), 800–1000 m, *Croat* 17235 (MO), *Luteyn & Kennedy* 1804 (DUKE), 1000 m, *Madison* 775 (GH, HUH); Río Pequení, 10–15 mi. upstream from hydrographic station by motor, *Dressler* 4884 (MO); betw. Tortí & Pilota del Toro, mtn. overlooking Tortí Arriba, *Folsom et al.* 5058 (MO); El Llano–Cartí rd., ca. 8 km N of turn-off, 300 m, *Churchill* 3804 (MO), 1000 ft., *Hammel & Kress* 13401 (DUKE). **San Blás:** forest SE of Puerto Obaldía, *Croat* 16818 (MO, SCZ); headwaters of Río Cangandi, trail from end of rd. past Los Altos de Pacora region of Cerro Jefé, 600–800 m, *Hammel & de Nevers* 13593 (MO). **Veraguas:** valley of Río Dos Bocas, 11 km

from Escuela Agrícola Alto Piedra (above Santa Fé) on rd. to Calovébora, forest along river, 450 m, *Croat* 27519 (MO).

20b. *Chlorospatha croatiana* var. *enneaphylla* (Grayum) Croat & L. P. Hannon, comb. & stat. nov. Basionym: *Chlorospatha croatiana* var. *enneaphylla* Grayum, Ann. Missouri Bot. Gard. 73: 466. 1986. TYPE: Colombia. Boyacá: El Humbo, 130 mi. N of Bogotá, 1933, *A. Lawrance* 794 (holotype, K!). Figure 17A–D.

Terrestrial or rarely hemiepiphytic herb, ca. 1 m tall or less; sap milky or transparent; internodes 0.8–3.3 cm long, drying 1–1.3 cm diam.; **petioles** 47–74 cm long, sheathed 1/2 to 2/3 of total length; **blades** deeply 5- to 9-lobed to \pm pedatisect, almost pedatisect; upper surface occasionally white maculate; all segments \pm narrowly elliptical, ovate or obovate, rarely lanceolate, weakly acuminate to \pm acute at apex, markedly narrowly confluent between segments, the confluent portion 0.5–3 mm wide; outer segments \pm acute or truncate at base on posterior side; posterior rib naked 4–8 cm per side; primary lateral veins 2 to 4 pairs, arising at 15°–35°, \pm straight to weakly arcuate; tertiary veins drying flat and \pm obscure on lower surface; reticulate veins drying obscure on lower surface. INFLORESCENCES 4 to 6 per axil; **spathe** 6.5–8 cm long; **spadix** 5.5–6.5 cm long, sessile; fertile staminate portion white or yellow; sterile staminate portion 5–10 mm long; pistils \pm laxly arranged, 3 to 4 across the axis (as viewed from above); sterile flowers irregularly lobed.

Phenology. Flowering is only known to occur in *Chlorospatha croatiana* var. *enneaphylla* in May, July, and August, with fruiting collections having been made in May and July.

Discussion. *Chlorospatha croatiana* var. *enneaphylla* is known from northwestern Colombia, in Antioquia, Boyacá, and Chocó departments, at 150–820 m elevation, in premontane wet forest, premontane rainforest, and transitional forest from premontane wet forest to tropical moist forest, and from Panama, in Chiriquí, Coclé, Darién, Panamá, and Veraguas provinces, at 710–1135 m elevation, in premontane wet forest, premontane rainforest, and lower montane rainforest. The six Colombian collections were made in only three areas separated by considerable distances. The type locality in Colombia is on the western slopes of the Cordillera Oriental in Boyacá Department, in premontane wet forest. The taxon was reported as abundant in the transitional forest area near the border between Colombia and Panama and would be expected to occur in Santander, Cundinamarca, and possibly Córdoba



Figure 17. *Chlorospatha croatianana* var. *enneaphylla* Grayum. —A. Habit showing blade adaxial surfaces, from *Croat & Grayum 60078* (MO). —B. Inflorescence beginning to open. —C. Inflorescence in side view, post-anthesis. —D. Inflorescence in frontal view, post-anthesis. B–D from cultivated plant at MO from *Croat 22815* from Panama.

departments in Colombia. *Chlorospatha* has not been reported from any of these departments.

Chlorospatha croatianana var. *enneaphylla*, a member of *Chlorospatha* sect. *Chlorospatha*, is terrestrial or hemiepiphytic and distinguished by its deeply 5- to 9-lobed, almost pedatisect, leaf blades with the segments narrowly attached at the base (0.5–2 cm wide at point of attachment), narrowly confluent or alate between segments, the confluent portion 0.5–3 mm wide, and occasionally white maculate. The taxon has only two to four pairs of primary lateral veins arising at 15°–35°, and usually only the midrib, major, and occasionally the secondary venation dry-raised on the lower surface, with the tertiary and reticulate venation more or less obscure. The taxon is also distinguished by its relatively long internodes (1–3.3 cm long) and its petiole, which is sheathed one half to two thirds of its length. The pistils are more or less laxly arranged (three or four across the horizontal axis, as viewed from above). The sterile flowers are irregularly lobed.

Grayum (1986) cited two sterile collections as *Chlorospatha croatianana* var. *enneaphylla*, Croat 49311 (MO) and Croat 55960 (MO), both from Chocó Department, on the western slopes of the Cordillera Occidental, at 285–825 m elevation. Subsequent collections of similar material indicate that these are better assigned to a new species, *C. morae* Croat & L. P. Hannon. *Chlorospatha croatianana* var. *enneaphylla* is a larger, more robust plant than *C. morae*, with a longer petiole, sheathed one half to two thirds of its length, and larger leaf blades with longer segments with two to four pairs of primary lateral veins on all segments. In *C. morae*, the petiole is sheathed about one half of its length and the segments have six to seven (eight, nine) pairs of primary lateral veins, except on the outermost segments, which have four or five pairs. Only the midrib, major, and some secondary venation are raised on the lower blade surface in *C. croatianana* var. *enneaphylla*, which lacks the conspicuous reticulate pattern found on the lower blade surface in *C. morae*, in which all venation dries raised or prominulous and weakly to moderately darker than the surface.

One 7-lobed specimen of *Callejas et al.* 4570 differs from the type in having more or less lanceolate segments (4 to) 4.2 to 5 times longer than wide versus 2.1 to 3 times longer than wide in typical specimens of variety *enneaphylla*. The leaf blade of the specimen is similar to that of *C. kolbii*, and this, combined with the more or less laxly arranged and similar pistils, would suggest a possible relationship between the two taxa.

Additional specimens examined. COLOMBIA. **Antioquia:** Mpio. Anorí, via Providencia, inlet at Algibes, along

Río Anorí, 310 m, *Callejas et al.* 4570 (COL, HUA, MO); Mpio. Remedios, Sitio Otú, 3 km N of Santa Isabela distr., vic. Los Lagos, 11 km from Remedios, via Remedios–Vegachi, in forest on bank of hwy., 820 m, *Callejas et al.* 4719 (HUA); Río Anorí valley, near Planta Providencia, betw. Dos Bocas & Anorí, 350–700 m, *Shepherd* 899 (COL, WIS); Anorí, Providencia area, betw. Providencia & Alhibe, 400–800 m, *D. Soejarto et al.* 4394 (HUA). **Chocó:** Mpio. Acandí, vic. Coquitál, 150–250 m, *Fonnegra et al.* 2914 (COL, HUA), 2928 (HUA). PANAMA. **Chiriquí:** Fortuna–Chiriquí Grande rd., 4.5–5 km N of dam over Fortuna Lake, 1100–1135 m, *Croat & Grayum* 60078 (MO). **Coclé:** vic. Alto Calvario, near sawmill above El Copé, 5.2 km above El Copé, 930 m, *Croat* 49172 (MO), 710–800 m, *Croat* 68752 (F, MO), 8 km N of El Copé, 750 m, *Maas et al.* 2740 (U). **Darién:** along headwaters of Río Tuquesa, ca. 2 km by air from Continental Divide, vic. of upper gold mining camp of Tyler Kittredge, *Croat* 27111 (MO). **Panamá:** Cerro Campana, W of Canal Zone, 1000 m, *Croat* 22815 (MO). **Veraguas:** Alto Piedra, vic. Santa Fé, along ridge extending to summit, 1 km from Escuela Círculo Alto de Piedra, on rd. to N going to Río San Luís, 800–950 m, *Croat* 66996 (M, MO).

21. *Chlorospatha cutucuensis* Madison, Selbyana 5(3–4): 354. 1981. TYPE: Ecuador. Morona-Santiago: Cordillera de Cutucú, ca. 25 km SE of Logroño, ca. 1700 m, 17 May 1979, *M. Madison* 6944 (holotype, SEL!; isotypes, MO!, QCA!, US!). Figure 12D.

Terrestrial herb, to 70 cm tall; stem erect, 20–30 cm long, remnants of old cataphylls persisting \pm intact at upper nodes; internodes 1.5–3 \times 1–2 cm, pale-medium brown, drying 0.5–1 cm diam., weakly glossy, pale to medium reddish brown; cataphylls 15–21 cm long, apex not known, drying weakly glossy, medium reddish or orangish brown. LEAVES 2 to 3, erect to erect-spreading; **petioles** 25–42.5 cm long, medium green, drying glabrous, matte to weakly glossy, medium to dark brown, usually darkest apically, sheathed 18–20 cm, ca. 2/3 of total length; sheath decurrent at apex; free portion 2–3.5 mm diam. midway (dry); **blades** held horizontally or drooping, sagittate-subhastate, (12–)20–29 \times (7–)15–22 cm, 1.1 to 1.3 times longer than wide, acute to weakly acuminate at apex, broadest at base, 1.5 to 1.6 times wider at base than across anterior lobe (measured tip to tip across posterior lobes), occasionally weakly constricted in area of petiole attachment, thin, moderately to conspicuously bicolorous; upper surface dull, medium green, drying matte, medium to medium-dark greenish brown; lower surface drying weakly glossy to semiglossy, occasionally gray-tinged brownish green, moderately paler; anterior lobe 16–20.5 \times 9.5–15 cm, 1.4 to 1.7 times longer than wide, 1.4 to 2 times longer than posterior lobes, broadest at base; posterior lobes directed somewhat outward, 8–14.5 \times 4–7 cm, 1.7 to 2.1 times longer than wide, narrowly

rounded at apex, rarely bluntly rounded, broadest at base, moderately inequilateral, the inner side narrower, weakly rounded at base, briefly to moderately attenuate and decurrent onto petiole; outer side 1.6 to 2.5 times wider than inner side midway, straight to weakly concave toward base; midrib drying weakly or entirely flattened on lower surface, weakly darker than surface, usually much darker toward base; **basal veins** 2 to 3 pairs, coalesced into a prominent posterior rib; primary lateral veins 4 to 5(6) pairs, arising at 15° – 60° , most acutely toward apex, weakly arcuate, drying \pm flattened on lower surface, weakly darker than surface, occasionally much darker toward base; secondary veins drying in part raised, otherwise mostly flattened on lower surface, weakly darker than surface; tertiary veins drying visible, distinct on lower surface, in part weakly darker than surface, otherwise concolorous; reticulate veins drying obscure; collective veins 3, the innermost arising from apex of posterior rib or uppermost lateral vein on inner side of posterior lobe, loop-connected with all preceding lateral veins, parallel to and ca. 3 mm from margin. INFLORESCENCES erect, 2 to 4 per axil; peduncle held within the sheath, 14–18 cm \times ca. 2 mm, drying yellowish tan in basal two thirds, dark brown apically, or entirely dark brown; **spathe** erect, 8.5–9 cm long, cuspidate at apex; spathe tube green, 2.2–2.8 cm \times 6–8 mm, drying matte, dark brown; spathe blade white or cream, ca. 5.7 cm long, ca. 1 cm wide (flattened), drying matte, dark brown, marcescent, erect after anthesis; **spadix** (details from pickled inflorescence) erect, 6–6.4 cm long, sessile, adnate to spathe ca. 4 mm at base, less than 1/4 of the length of pistillate portion; pistillate portion cream to pale yellow, 2 cm \times 3–5 mm; fertile staminate portion white, 3.5–4 cm \times 3–4 mm, bluntly acute at apex, weakly thicker than broad, broadest at base, tapering; sterile staminate portion cream, 7–8 \times 4 mm; pistils weakly coherent, 4 to 5 across the axis (viewed from above), 1–1.2 mm long; ovaries cream, ovoid to \pm cylindrical, 1.5–2 mm diam., occasionally obtusely truncate at apex, (2)3- to 4-locular, with pseudoaxile placentation in basal 1/2; ovules 4 to 10 per locule, anatropous, biseriate; funicle shorter than ovule; style Type 2 (Fig. 1), 0.3–0.5 \times 0.8–1 mm, comprising ca. 1/4 of the length of pistil, weakly broadest at base, prominently narrower than ovary apex, briefly irregularly attenuate, usually \pm wrinkled, occasionally weakly shorter than and surrounding the stigma, with numerous red chromoplasts; **stigma** yellow, ca. 0.5 mm diam., elevated on style, broadest at apex; synandria ca. 1 \times ca. 1.5 mm, \pm elongated in direction of axis in basal 1/2 of spadix, coherent, truncate, 3- to 4-lobed, 3- to 4-androus (mostly 4); sterile flowers ca. 1 \times 1–3 mm, \pm

elongated in direction of axis, coherent, truncate, subprismatic to occasionally irregularly lobed, in 3 whorls. INFRUCTESCENCE (immature) 2.5 cm \times 8 mm; berries white, ca. 3 mm diam.; seeds 3 to 5 per berry (mostly 3), 1.5 mm long, ovoid, striate.

Phenology. Flowering is only known to occur in *Chlorospatha cutucuensis* during the months of May, September, and November. It is likely that flowering occurs during some of the intervening months. Fruiting is known to occur only during the month of November.

Discussion. *Chlorospatha cutucuensis* is known only from lower montane wet forest in an area near Logroño in Morona-Santiago Province, Ecuador, on the western slopes of the Cordillera de Cutucú, east of the Andes, at 1700–1900 m elevation. The species has not been collected since the type was collected except once (*Madison et al.* 3530), but it would be expected to occur elsewhere in the Cutucú and perhaps nowhere else, the Cutucú being a region noted for a high level of endemism in species of Araceae.

Chlorospatha cutucuensis is a member of *Chlorospatha* sect. *Orientales* and is characterized by its dull, medium green, somewhat triangular, sagittate-subhastate leaf blades that dry semiglossy and conspicuously smooth on the lower surface, with all venation glabrous and flattened. This is noteworthy because the blades of all other known species from the area east of the Andes in Ecuador, except *C. portillae* and *C. sizemoreae*, are reticulate and narrowly colliculate along all orders of venation on the lower surface and dry less glossy, with all venation raised, prominulous, or otherwise visibly distinct. *Chlorospatha cutucuensis* is a large plant compared to most species from the eastern slopes and is also distinguished from those species by its long petiole sheathing (ca. two thirds of total length), long peduncles (14–18 cm long), and synandria that are evenly lobed and truncate at the apex. The synandria of *C. cutucuensis* are similar to those of all species from the western slopes, but to only four species from the eastern slopes, in *Chlorospatha* sect. *Orientales*: *C. engleri*, *C. limonensis*, *C. portillae*, and *C. sizemoreae*. Although the species could not be confused, *C. cutucuensis*, *C. portillae*, and *C. sizemoreae* are the only members of *Chlorospatha* sect. *Orientales* with attenuated styles. The style of *C. cutucuensis* differs from that of the other two species in frequently having the attenuated portion wrinkled, occasionally forming a conspicuous “collar” around most of the stigma, with only the apex of the stigma exposed above the “collar” (at least in pickled material). The style is smooth and unwrinkled in *C. portillae* and *C. sizemoreae* and the stigma fully exposed.

Chlorospatha cutucuensis would be most easily confused with *C. yaupiensis*, with which it is sympatric in the area near Logroño in the Cordillera de Cutucú (cf. discussion under *C. yaupiensis*). Both species have long peduncles and leaf blades of similar shape, but the posterior lobes in *C. yaupiensis* are broader, only 1.5 times longer than wide, usually shorter, more broadly rounded at the apex, and lack the tapering aspect usually observed in those of *C. cutucuensis*. Pale linear cellular inclusions were observed in the developing blade of *C. yaupiensis* but not in that of *C. cutucuensis*. The lower blade surface is reticulate and dries matte in *C. yaupiensis*, with all orders of venation more or less raised or prominulous and crispy-puberulent to granular-puberulent, thus differing from that of *C. cutucuensis*, which dries semiglossy, with all venation glabrous and flattened.

Madison (1981) reported that the pistils of *Chlorospatha cutucuensis* were more closely crowded together than those of other species of *Chlorospatha* and suggested that this feature placed it somewhat closer to *Xanthosoma*. Numerous collections of different species of *Chlorospatha* have since been made, revealing that this feature is common and not the exception. The ovaries of *C. cutucuensis* are only weakly coherent and clearly distinct from one another, with the styles narrower than the ovary and neither coherent nor weakly connate, thus differing from the pistils of *Xanthosoma*, in which the ovaries and styles are coherent and the styles are as broad as the ovary.

Additional specimen examined. ECUADOR. **Morona-Santiago:** Cordillera de Cutucú, Logroño–Yaupi trail, 1750–1900 m, *Madison et al.* 3530 (SEL, US).

22. *Chlorospatha dodsonii* (G. S. Bunting) Madison, *Selbyana* 5(3–4): 352. 1981. Basionym: *Caladiopsis dodsonii* G. S. Bunting, *Ann. Missouri Bot. Gard.* 50: 28. 1963. TYPE: Ecuador. Pichincha: along Río Baba, 28 km S of Santo Domingo de los Colorados, 350 m, 3 Nov. 1961, *C. Dodson & Thien* 1190 (holotype, MO-1782096!; isotypes, B not seen, CAS not seen, F!, K!, NY!, QCA!, US!). Figures 2A–F, 18A–D.

Terrestrial herb, rarely hemiepiphytic, to 1 m tall; stem usually erect, 25–50 cm tall, but can be decumbent or rarely hemiepiphytic and to 80 cm long, cylindrical, producing bulbils randomly along its length; bulbils solitary, 3–10 × 2–4 mm, longer than broad, sparsely covered in medium brown fibers; sap milky; internodes 1–2(–3) × 1–4 cm, weakly scurfy, matte, medium brown, drying matte, dark brown; cataphylls ultimately deciduous, 10–43 cm long,

obtuse with acumen at apex, obtusely 1-ribbed abaxially, green, drying weakly glossy, dark brown. LEAVES 4 to 8, erect-spreading; **petioles** 30–90 cm long, moderately firm, rarely weakly spongy, glabrous, matte, entirely purplish or pale, medium or dark green, or in part medium to dark green and purplish near base, drying matte to weakly glossy, occasionally semiglossy, medium-dark to dark brown, sheathed 13–46(–55) cm, ca. 1/2 to 2/3 of total length, occasionally to 3/4, usually less than 1/2 of its length when not in flower; sheath decurrent at apex, rarely free-ending, the margins frequently conspicuously narrowly undulate; free portion 0.5–1 cm diam. midway, entirely terete or in part terete and otherwise obtusely C- or D-shaped toward apex and occasionally obtusely sulcate at apex, occasionally entirely obtusely D-shaped, with obtuse medial rib; **blades** held ± horizontally, hastate to markedly hastate, 21–42 × 19–44.5 cm, usually weakly wider than long, gradually to occasionally abruptly acuminate at apex, broadest at base, 1.8 to 2.9 times wider at base than across anterior lobe (measured tip to tip across posterior lobes), thin to thinly coriaceous, rarely subcoriaceous, weakly to moderately bicolorous; upper surface weakly to moderately wrinkled, matte to semiglossy or velvety, dark green, drying matte to weakly glossy, occasionally semiglossy, medium-dark to dark greenish brown or olive-green, occasionally brownish green; lower surface reticulate, obscurely narrowly colliculate along some venation, matte to weakly glossy, occasionally semiglossy, drying weakly to moderately paler, occasionally gray-tinged green; anterior lobe 16–33.5 × 9–18.5 cm, (1.2)1.3 to 2 times longer than wide, 1.1 to 1.7 times longer than posterior lobes, broadest at or below middle, moderately to markedly constricted at base, ± symmetrical; posterior lobes directed prominently outward, frequently weakly toward apex on drying, 9.5–24 × 3.8–10.5 cm, 2.1 to 2.8(to 3.4) times longer than wide, acute to bluntly acute or occasionally ± acuminate at apex, broadest at or below middle, usually markedly constricted at base, weakly to moderately inequilateral, the outer side narrower, ± straight toward base; inner side (1)1.1 to 1.6 times wider than outer side midway, moderately to broadly rounded toward base and briefly attenuate onto posterior rib; midrib and major venation prominently round-raised on lower surface, matte, weakly paler than surface, drying raised or occasionally in part weakly flattened, weakly to moderately darker than surface, rarely paler; midrib sunken on upper surface; **basal veins** (4)5 to 7(8) pairs, coalesced into a prominent posterior rib; posterior rib naked 0.2–1.5 cm per side; primary lateral veins (5)6 to 8(9) pairs, arising at (30°–)40°–60°, most acutely toward apex,

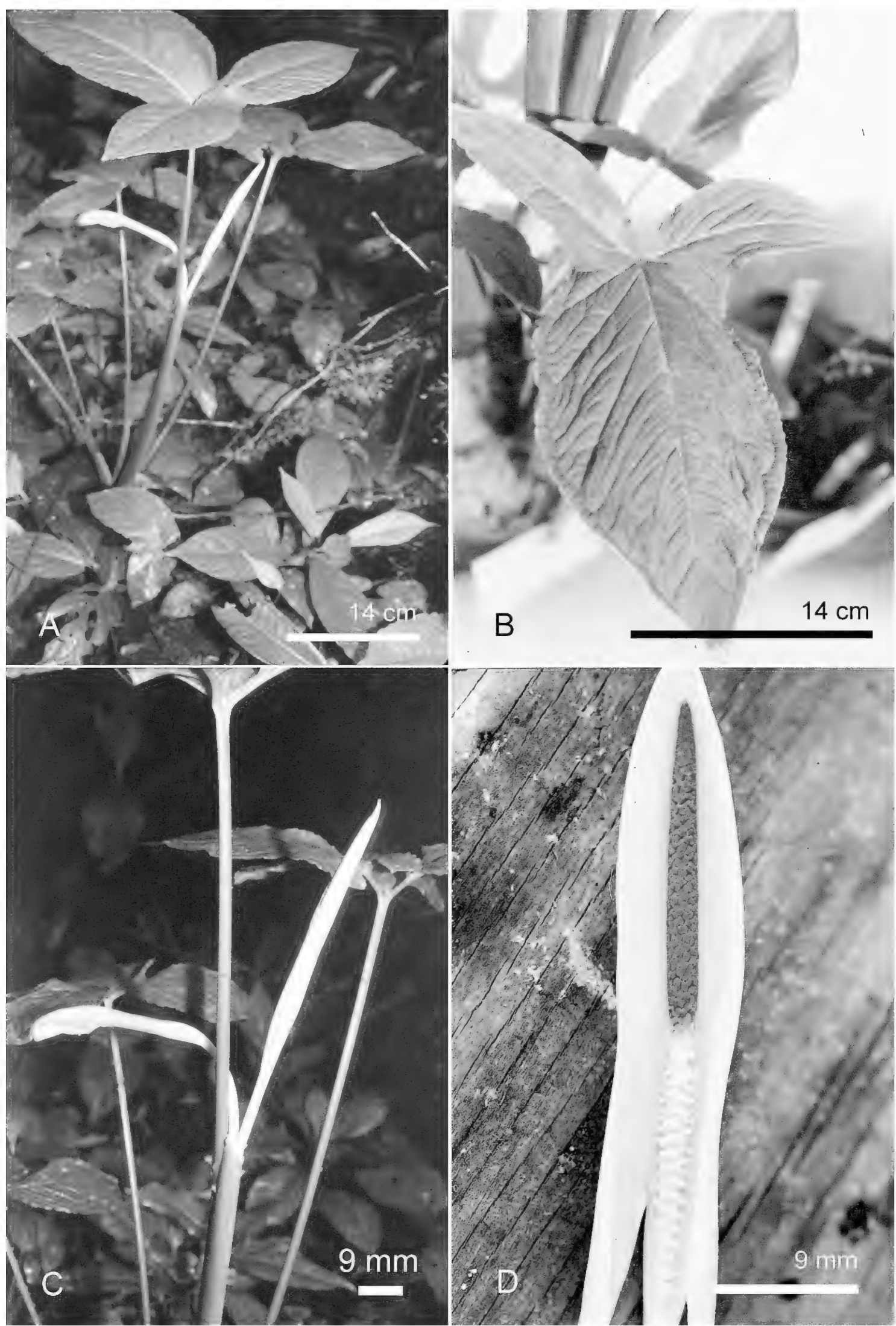


Figure 18. *Chlorospatha dodsonii* (G. S. Bunting) Madison. —A. Fertile habit, *Croat 73039* (MO). —B. Leaf blade adaxial surface, cultivated plant, from *Grayum & Zamora 9427* (MO). —C. Petiole group, the central one, with the inflorescence to the right pre-anthesal, from *Croat 73039* (MO). —D. Inflorescence at full anthesis, with spathe tube cut open, from *Dodson & Dodson 6755* (MO).

straight or weakly to moderately arcuate, quilted-sunken on upper surface; secondary veins quilted-sunken on upper surface, moderately to prominently raised and concolorous on lower surface, drying raised, concolorous to weakly darker than surface, occasionally weakly paler; tertiary veins entirely or in part weakly sunken on upper surface, moderately to prominently raised or prominulous on lower surface, \pm concolorous, drying raised or prominulous, concolorous to weakly darker than surface; reticulate veins raised or prominulous on lower surface, \pm concolorous, drying prominulous or weakly to moderately raised, concolorous to weakly darker than surface; collective veins 3(4), the innermost arising from one of the lowermost lateral veins on inner side of posterior lobe, loop-connected with all preceding lateral veins, weakly to moderately scalloped, 2–9(–11) mm from margin. INFLORESCENCES erect, 2 to 4 per axil, emitting a sweet-soapy fragrance at anthesis; inflorescence cataphyll 1-ribbed abaxially; peduncle held within the sheath, (26–)30–59 cm \times 2–4 mm, cylindroid, thicker than broad, narrowing toward base, semiglossy, greenish to yellow-green cream, drying matte to weakly glossy, medium to dark brown, rarely greenish; **spathe** erect, matte, cream or greenish cream to pale yellow-green or greenish white on outer surface, (11–)13–20 cm long, frequently conspicuously longer than spadix (1–3.5 cm longer), lanceolate, cuspidate or obtuse with acumen at apex, opening 1/2 to 2/3 of its length and \pm funnel-shaped at anthesis, \pm broadly on the blade; spathe tube semiglossy and paler on inner surface, occasionally with weakly darker longitudinal veins, 6–9.5 cm \times (4–)6–12 mm, occasionally thicker than broad, drying matte, dark brown to reddish brown on outer surface, rarely tan, weakly glossy and weakly paler on inner surface, rarely matte; spathe blade matte and weakly paler on inner surface, 6.5–14 cm \times 7–12 mm, to 3 cm wide (flattened), obtusely 1-ribbed abaxially, acutely so in apical 1.5 cm, drying matte, dark tan to brown or reddish brown on outer surface, weakly paler on inner surface, marcescent, erect after anthesis; **spadix** erect, (10.5–)12–16.5 cm long, sessile, adnate to spathe 4.8–8.8 cm at base, usually entire length of pistillate portion, rarely slightly less or also onto most of sterile portion; axis white to greenish white; pistillate portion cream, rarely weakly orangish yellow-tinged cream, (5–)5.5–9 cm \times 5–8 mm, flattened, broader than thick, broadest toward apex; fertile staminate portion matte, bright orange, rarely reddish brown or white, or in part bright orange and otherwise green (at apex), 5–7.2 cm \times 4–7 mm, bluntly acute at apex, occasionally thicker than broad, tapering, drying dark orangish brown; sterile staminate portion entirely cream-colored or in part cream toward

base and creamy yellow to medium yellow-orange at apex, 2–7(–10) \times ca. 4 mm, \pm cylindrical, occasionally with axis naked 1–2 mm at base; pistils \pm laxly arranged, ca. 4 across the axis (viewed from above), 2.2–3.2 mm long; ovaries white to cream, obtusely conical, frequently truncate at apex, 1–1.5 \times 2–2.5 mm, drying pale tan to \pm whitish, 3- to 4-locular, with axile or subaxile placentation; ovules small, to 14 per locule, hemianatropous, biseriate; funicle as long as ovule or weakly shorter; style Type 8 (Fig. 1), 1.5–2 \times ca. 1.5 mm, comprising 1/2 to 2/3 or slightly more of length of pistil (attenuate portion to 2 mm long), with red chromoplasts, the margins not coherent with those of adjacent styles; **stigma** translucent white to creamy white, 0.6–0.8 mm diam., broadest apically and truncate, markedly elevated on style; synandria ca. 1–2 \times 2–3 mm, coherent, truncate, deeply 2- to 5-lobed, 2- to 5-androus (mostly 3 to 4), occasionally lacking microsporangia in apical 2 to 3 whorls; pollen exine smooth (see Fig. 2); sterile flowers ca. 1 \times ca. 1 mm, or 1–1.5 \times 1.5–2.3 mm diam. and \pm elongated in direction of axis, \pm coherent, truncate, subprismatic, in 1 to 3(4) whorls (occasionally with none present). INFRUCTESCENCE nutant (apex directed downward), green, drying 8–13 \times 1–1.3 cm, matte to weakly glossy, dark brown to reddish brown; berries whitish, 4–7 mm diam. (dry).

Phenology. Flowering in *Chlorospatha dodsonii* has been reported or observed in all months of the year except January and May, and is likely to occur in those months as well. Inflorescences emerge in slow progression, with several days between anthesis of one inflorescence and emergence of the next inflorescence at the apex of the petiole sheath. In cultivation, flowering is not continuous but periodic. Fruiting is reported for the month of June.

Discussion. *Chlorospatha dodsonii* is widespread on the western slopes of the Andes in northern Ecuador, mainly in premontane wet forest, but also is found in tropical wet forest and premontane rainforest in Carchi, Cotopaxi, Esmeraldas, and Pichincha provinces and in premontane moist forest in Manabí Province. The species would be expected to occur to the north into Colombia and into other provinces to the south in Ecuador, particularly Los Ríos, which borders several collection sites in Cotopaxi and Pichincha.

Chlorospatha dodsonii is a member of *Chlorospatha* sect. *Occidentales* and is known from a considerable range in elevation (100–1500 m); however, there is little or no variation in distinguishing characters throughout this range, one being the fine reticulate pattern of the veins on the lower

surface of the leaf blades, with all orders of venation more or less raised. This pattern is conspicuous in both living and dried material, which, combined with its prominently hastate blades, make it easily distinguishable from all other species with which it might be confused, even when sterile. This character appears to be somewhat more pronounced in the higher elevation collections. *Chlorospatha dodsonii* is also distinguished by its large inflorescence, bright orange synandria, and its extraordinary style that represents an extreme in the genus. The style comprises ca. two thirds of the length of the pistil, with the attenuate portion as much as 2 mm long. Some inflorescences of *C. dodsonii* are the largest known in the genus, the spathe being as much as 20 cm long, though usually somewhat shorter.

Chlorospatha dodsonii could possibly be confused with *C. ilensis* in the sterile state, both occurring in Cotopaxi, Pichincha, and probably Los Ríos provinces in Ecuador. Like *C. dodsonii*, *C. ilensis* has prominently hastate leaf blades with both the anterior and posterior lobes conspicuously constricted at the base (see discussion under *C. ilensis*).

Chlorospatha dodsonii would be most easily confused with *C. litensis*, with which it is sympatric in the Lita–San Lorenzo region of Esmeraldas Province. The stems of *C. litensis* are smooth and green, unlike those of *C. dodsonii*, which are somewhat scurfy and always tan to brown. Both species have markedly hastate leaf blades and bright orange synandria. The lower surface of the leaf blade of *C. litensis* either lacks the conspicuous reticulate pattern that is so characteristic of *C. dodsonii*, or has it weakly and inconsistently expressed in dried material, and the midrib and major veins are usually darker than the surface and obtusely ribbed. *Chlorospatha dodsonii* differs in having the midrib and major veins smooth (not ribbed) and paler than the lower surface. The petiole of *C. litensis* is obtusely many-ribbed abaxially, sheathed three fourths or more of its length, with the sheath free-ending at the apex and the free portion usually sharply D-shaped, with the margins erect and acute most or all of its length. The petiole of *C. dodsonii* is smooth (not ribbed), sheathed one half to two thirds of its length, with the sheath usually decurrent at the apex and the free portion either entirely terete or in part terete and obtusely D- or C-shaped toward the apex. The inflorescence of *C. litensis* is consistently smaller than that of *C. dodsonii* (in plants of comparable size), with the pistillate portion of the spadix less than half as long as the maximum length observed in *C. dodsonii*, weakly stipitate, and adnate to the spathe only one half to three fourths of its length. The

pistillate portion of *C. dodsonii* is sessile and adnate most or all of its length, and the peduncles are usually no more than two thirds as long as the petiole (rarely three fourths as long). In *C. litensis*, the peduncles are usually nearly as long as or longer than the petiole. The sterile staminate spadix of *C. litensis* is unusually long relative to total spadix length, (1–)1.5–2.5 cm long, with the sterile flowers arranged in five to seven whorls, thus differing from that of *C. dodsonii*, which is unusually short, typically 2–7 mm long, with the sterile flowers arranged in only one to three whorls or occasionally with none present. The spadix of *C. litensis* is consistently smaller than that of *C. dodsonii*, with the pistillate portion more densely flowered, approximately half as long as the shortest encountered in *C. dodsonii*, weakly stipitate and adnate to the spathe only one half to three fourths of its length. The pistillate portion in *C. dodsonii* is laxly flowered, sessile, and adnate most or all of its length. The sterile staminate portion is unusually long in *C. litensis*, relative to total spadix length, (1–)1.5–2.5 cm long, usually with the axis naked up to 1 cm at the base, thus differing from that of *C. dodsonii*, which is unusually short, 2–7 mm long (on much longer spadix), with the sterile flowers in only one to three whorls or occasionally with none present. The sterile flowers of *C. litensis* are arranged in five to seven whorls. A key difference lies in the morphology of the style. In *C. litensis*, the style (Type 9, Fig. 1) comprises only one third of the length of the pistil, with the margins weakly coherent with those of adjacent styles. The style (Type 8, Fig. 1) of *C. dodsonii* comprises one half to two thirds or more of the length of the pistil, with the margins of adjacent styles not at all coherent with those of adjacent styles.

Chlorospatha dodsonii could also be confused with *C. mansellii*, especially in dried material, both having leaf blades that dry hastate. The species are sympatric in the Lita–San Lorenzo Region of northwestern Ecuador and are contrasted in the discussion for *C. mansellii*.

Although the bright orange, fertile staminate spadix of *Chlorospatha dodsonii* is a key character for the species, in one collection from Manabí, *Clark et al.* 6745, it is reported as white. In all other respects, both floral and vegetative, the collection accords with *C. dodsonii*, most significantly in the morphology of the style. *N. Pitman* 1334 and *De Links & Robles* 121 are from the same general area in Manabí and report this portion of the spadix as either orange and green or entirely orange. All three collections accord well with *C. dodsonii*, but interestingly, the leaf blades dry somewhat grayish green on the lower surface. The label notes from a

collection made in Pichincha (Croat 73039) possibly explain the discrepancy in spadix color, reporting that the spadix is white before anthesis and otherwise orange. However, several examinations of pre-anthesis inflorescences (in living material of other collections) in the earliest stages of development, did not confirm this. The synandria examined were paler to much paler orange, but not white.

Madison 4179 is unusual in having the style weakly orangish, yellow-tinged cream.

Croat et al. 84154 (MO), a sterile collection from Esmeraldas Province, is possibly this species. The label notes report the tertiary venation as prominently raised, but on drying, the reticulate pattern on the lower blade surface is very weak or completely lacking in some areas. Another collection that might be this species is *Croat 55831* (CM, MO), a small, juvenile collection from Cotopaxi Province, described as bullate on the label notes, a condition not observed in *C. dodsonii*.

Additional specimens examined. ECUADOR. **Carchi:** San Marcos, 600 m, *S. Thompson et al. 780* (CM, MO). **Cotopaxi:** Teneuerte, Río Pilaló, Km. 52–53, Latacunga, 750–1300 m, *Dodson & Gentry 12216* (SEL), 750–900 m, *C. & P. Dodson 12930* (MO, SEL), Km. 55, along the hwy., to N of mtn., 850–1000 m, *Dodson et al. 14408* (MO, QCNE). **Esmeraldas:** San Lorenzo Cantón, along Lita–San Lorenzo rd., 40.1 km W of Lita, 350 m, *Croat 72326* (K, MO); vic. Lita, 550–560 m, *Madison et al. 5065* (SEL); Quinindé, Esmeraldas–Quinindé, Herrera–El Páramo hwy., Santa Isabela, Bilsa Biol. Res. 580 m, *W. Palacios et al. 13522* (MO, QCNE); Quinindé, Bilsa Biol. Re., 35 km W of Quinindé, 5 km W of Santa Isabela, along Dogala trail, 400–600 m, *N. Pitman & M. Bass 954* (MO, QCNE). **Manabí:** Pedernales Cantón, Cerro Paja de Pájaro, 10 km E of Pedernales, Finca Aroyo, 300–700 m, *J. Clark et al. 6745* (CAS, MO, QCNE), E side of main trail, 300–520 m, *T. Delinks & C. Robles 121* (MO, QCNE); Bosque Prot. Cerro Paja de Pájaro, ca. 10 km E of Pedernales, E slope of mtn., below S peak, 400–700 m, *N. Pitman 1334* (MO, QCNE). **Pichincha:** Tinalandia, 9.6 km E of Santo Domingo, S of Aloag–Quito hwy., above Río Toachi, 700 m, *Croat 55722* (MO, QCA); Santo Domingo, vic. La Centinela, 0.2 km past Escuela Mixta La Centinela, along trail to lt. of rd., 13 km E from main Santo Domingo–Quevedo hwy. in Patricia Pilar, 1000 m, *Croat 73039* (CM, M, MO, QCNE); vic. Santo Domingo, vic. Peripa, SW of Santo Domingo, 250 m, *Croat & M. Nuñez 82094* (AAU, MO, NY, QCNE); San Miguel de los Bancos Cantón, along Nanegalito–Mindo rd., 16.5 km SSW of Nanegalito, 1500 m, *Croat et al. 82746, 82749* (MO, QCNE); along rd. to Chittoa, departing main Quito–Santo Domingo hwy. at Km. 44, 0.4 km N of main hwy., *Croat 82836* (B, MO, NY, QCNE); along ridge-line near La Centinela at Km. 12 on Patricia Pilar–Flor de Mayo rd., Mts. de Ila, 600 m, *C. & H. Dodson 6755* (CAS, F, MO, RPSC, SEL); Coop. Santa Marta #2, at Km. 3 W of bypass around Santo Domingo, 530 m, *C. Dodson et al. 8530* (MO, SEL); outskirts of Santo Domingo, Río Chiguilpe, ca. 550 m, *Gentry et al. 24715* (MO); E side of Río Lelia, ca. 16 km (as crow flies) SE of Santo Domingo, 800 m, *Grayum & Zamora 9427* (K, MO); Res. Endesa,

turn-off at Km. 113 on Quito–Puerto Quito rd., small stream 0.5 km S of Endesa houses, 450 m, *Hammel & Wilder 17225* (MO); vic. Alluriquín, 900 m, *Madison 4015* (SEL); Quito–Puerto Quito hwy., Km. 113, 10 km N of main hwy., 800 m, 0°05'N, 79°02'W, 28 Feb. 1984, *J. Rodríguez 252* (MO, QCA); Res. Endesa, Quito–Nono–Tandayapa–Puerto Quito hwy., Km. 113, 800 m, *V. Zak 1601* (QCA).

Cultivated specimens examined. ECUADOR. **Pichincha:** Mts. de Ila, 1977, *Madison 4179* (SEL, cult. from *C. & H. Dodson 6755*; SEL live acc. 1977–2728).

23. *Chlorospatha engleri* Croat & L. P. Hannon, sp. nov. TYPE: Ecuador. Morona-Santiago: Parque Nac. Sangay, 28.6 km W of Proaño, on Macas–Riobamba rd., near river crossing, S side of rd., 1659 m, 2°14'31''S, 78°16'40''W, 13 Aug. 2002, *Croat, L. P. Hannon & P. Schmidt 86559* (holotype, MO-5763472!; isotypes, AAU!, B!, CAS!, COL!, F!, GH!, HUA!, K!, M!, MEXU!, NY!, PMA!, QCA!, QCNE!, S!, SEL!, UB!, US!, VEN!). Figure 19A–D.

Herba usque ad 50 cm; internodia (1.5–)2–4.5 × to 1.9 cm; cataphylla 5–17 cm longa. Petiolus 23–37.5(–40) cm longus; lamina foliaris triangulo-sagittata vel subhastata, 14.5–27 × 6–16 cm, lobis posterioribus 3.5–11.5 × 3–6.5 cm, nervis basalibus utroque 3 vel 4, nervis primariis lateralibus utroque 3 vel 4. Inflorescentiae 3 vel 4 in quaque axilla; pedunculus (8–)9.5–12.5 cm × 1–2 mm (in sicco); spatha 3.7–4.5 cm longa tubo 1.5–2 cm × 3–4 mm, lamina 2.2–2.4 cm longa, 4–6 mm diam.; spadix erectus, 3.3–3.7 cm longus.

Terrestrial herb, to 50 cm tall, in small colonies; stem decumbent, erect to 15 cm, remnants of old leaf bases persisting as short fragments at all nodes, with remnants of old cataphylls persisting (or not) semi-intact and ± fibrous or as linear fibers, the fibers pale to medium brown; internodes (1.5–)2–4.5 × to 1.9 cm, semiglossy, olive-green, occasionally with closely spaced longitudinal grooves near nodes, drying 5–10 mm diam., matte, medium greenish brown to brown; cataphylls 5–17 cm long, acuminate or obtuse with acumen at apex, green, obtusely or acutely 1-ribbed abaxially, becoming fibrous, drying matte, medium yellowish brown. LEAVES 3 to 6, erect-spreading; **petioles** 23–37.5(–40) cm long, matte, pale to medium green, weakly to moderately darker purplish speckled in transverse bands, most prominently so toward base, drying matte, medium greenish brown, sheathed 9–18.5 cm, 1/3 to 1/2 of total length; sheath erect-spreading, in-rolled along margins, free-ending or decurrent at apex; free portion 2–4 mm diam. midway (dry), obtusely C-shaped, weakly sulcate, entirely sparsely crispy-puberulent or only in apical 1/2, finely many-ribbed near apex; **blades** triangular-sagittate to subhastate,



Figure 19. *Chlorospatha engleri* Croat & L. P. Hannon, from the type collection *Croat et al.* 86559 (MO). —A. Entire live type plant with immature and mature infructescences (blades with abaxial surfaces exposed). —B. Leaf blade adaxial surfaces. —C. Stem with inflorescence at left in anthesis. —D. Stems with anthesal inflorescence at left and mature infructescence to right.

occasionally narrowly ovate in young plants, 14.5–27 × 6–16 cm, 1.5 to 2.5 times longer than wide, weakly acuminate or acute at apex, usually broadest at base, occasionally weakly broadest across anterior lobe, 1.1 to 1.2 times wider at base than across anterior lobe (measured tip to tip across posterior lobes), weakly to moderately or not at all constricted on one side in area of petiole attachment, thinly coriaceous, moderately bicolorous, the margins crispate-undulate; upper surface bullate, matte-subvelvety, dark green, drying matte, dark olive-green, occasionally greenish brown; lower surface reticulate, matte, weakly narrowly colliculate along all venation, drying weakly glossy to semiglossy, weakly to moderately paler; anterior lobe 11.2–18(–20.5) × 6–14 cm, 1.2 to 1.8(to 2.1) times longer than wide, 1.5 to 2.7(to 3.1) times longer than posterior lobes, broadest below middle, weakly to moderately inequilateral, with one side 0.5–1.8 cm wider than opposite side; posterior lobes directed toward the base or frequently somewhat outward, 3.5–11.5 × 3–6.5 cm, (1 to) 1.3 to 1.6 times longer than wide, narrowly rounded at apex, broadest at base, weakly to moderately inequilateral, the inner side narrower, ± acute toward base, decurrent onto petiole; outer side 1.6 to 2.2 times wider than inner side midway; midrib and major venation narrowly, deeply sunken on upper surface and weakly paler than surface, narrowly round-raised on lower surface, minutely obtusely ribbed, granular-puberulent and in part sparsely crispy-puberulent (mainly toward base), concolorous to weakly paler than surface, drying weakly raised to ± flattened, weakly to moderately darker than surface; **basal veins** 3 to 4 pairs, coalesced into a prominent posterior rib or loosely coalesced into a short posterior rib 2.5–4.5 cm long, with 4 to 7 veins branching off, the first free to the base, 2 to 3 acroscopic, 2 to 4 basiscopic; primary lateral veins 3 to 4 pairs, arising at 25°–45°(–70°), most acutely toward apex, weakly to moderately arcuate, occasionally prominently arcuate or ± straight; secondary and tertiary veins narrowly quilted-sunken on upper surface and concolorous, weakly raised on lower surface, granular-puberulent and in part sparsely crispy-puberulent, weakly darker than surface, drying weakly raised, weakly to moderately darker than surface; reticulate veins conspicuous on lower surface, weakly prominulous, weakly darker than surface, drying prominulous, weakly to moderately darker than surface; collective veins 3 to 4, the innermost arising from apex of posterior rib or from a lateral vein on inner side of posterior lobe, ± parallel to margin to prominently scalloped, 3–19 mm from margin. **INFLORESCENCES** erect, 3 to 4 per axil, emitting a spicy-sweet

fragrance at anthesis; sympodium held within a sympodial cataphyll; sympodial cataphyll 9–14 × 1–2 cm, acuminate at apex, 1-ribbed abaxially; peduncle curved, (8–)9.5–12.5 cm × 1–2 mm (dry) (to 15 cm long in fruit), moderately flattened, matte, pale to medium green, drying matte, medium greenish brown; **spathe** erect, pale to pale-medium green, 3.7–4.5 cm long, oblanceolate, cuspidate at apex, opening narrowly most of its length at anthesis, ± broadly on the blade, the margins directed outward; spathe tube 1.5–2 cm × 3–4 mm, drying matte, dark brown; spathe blade 2.2–2.4 cm × 4–6 mm, drying matte, medium to dark brown, marcescent, erect after anthesis; **spadix** erect, 3.3–3.7 cm long, ca. 4 mm shorter than spathe, sessile, adnate to spathe 7 mm at base, ca. 1/2 of the length of pistillate portion; pistillate portion yellowish white, 1.5–1.7 cm × 2–3 mm, broadest below middle; fertile staminate portion creamy white, 1.8–2 cm × 3.5–4 mm, narrowly rounded at apex, ± cylindrical; sterile staminate portion creamy white, ca. 3 × 2.6 mm; pistils weakly coherent, 3 to 4 across the axis (viewed from above), ca. 1 mm long; ovaries ca. 0.7 × 1.3–2 mm, ± cylindrical or obtusely obconical, broadly depressed medially, (2)3- to 4-locular (mostly 3), with axile or subaxile placentation; ovules 8 to 14 per locule, 0.225 mm long, hemianatropous, biseriate; funicle 0.2 mm long, shorter than ovule, lacking glands; style Type 1 (Fig. 1), 1.3–2 mm diam., as broad as ovary apex (possibly weakly attenuate medially), the margins obscure and weakly or not at all coherent with those of adjacent styles; **stigma** whitish, ca. 1 mm diam., sessile, subrounded, button-shaped (possibly weakly elevated on style); synandria 1–1.5 × 1.2–2 mm, coherent, truncate, prominently and deeply 2- to 3(4)-lobed to the center, the lobes separate apically, the margins deeply sinuate, 2- to 3(4)-androus (mostly 3), staminal pores borne along distal margins; stamens ± reniform at apex, obtusely V-cleft on outer margin, emarginate on lateral margins; pollen sacs distributed along lateral margins; sterile flowers ca. 1 × 1–1.5 mm, coherent, truncate, subprismatic (viewed from above) or lobed (as per synandria), inequilateral, the stipe nearly as long as the thickened body, this inequilateral and directed toward apex, the apical portion curved, much broader than thick, in 3 whorls. **INFRUCTESCENCES** 2.2–4.5 cm × 6.5–10 mm, matte, dark purple on outer surface, semiglossy and greenish on inner surface, drying matte, dark brown, purplish or purplish black; berries ca. 1.5 × 2–3.5 mm, pale creamy-green.

Phenology. Flowering and fruiting are only known to occur in *Chlorospatha engleri* during the

month of August. Inflorescences are fragrant and emerge in quick succession, each reaching anthesis approximately one to three days after anthesis of the preceding inflorescence.

Etymology. *Chlorospatha engleri* is named for Dr. Adolf Engler (1844–1930), premiere aroid specialist and prodigious monographer of aroid genera, who first recognized and published the genus *Chlorospatha* in 1878.

Discussion. *Chlorospatha engleri* is known only from the type collection made 28.6 km west of Proaño, near a small river on the Macas to Riobamba road in the Parque Nacional Sangay in Morona-Santiago Province, Ecuador, on the eastern slopes of the Andes at 1659 m elevation. The montane rainforest at the type locality was being cut as the collection was being made and had been completely felled when the site was revisited two weeks later. The species would be expected to occur elsewhere within the park, which covers a large area, also to the west and south in Chimborazo and Cañar provinces, to the north in Tungurahua and Pastaza provinces, and possibly at similar elevations in westernmost Napo Province.

Chlorospatha engleri, a member of *Chlorospatha* sect. *Orientales*, is found in small colonies and is distinguished by its moderately long internodes (2–4.5 cm long) and triangular-sagittate to subhastate leaf blades that are bullate, matte-subvelvety, dark green on the upper surface and reticulate and matte on the lower surface, with all abaxial venation more or less raised or prominulous, and the midrib and major venation finely ribbed, granular-puberulent, and in part sparsely crispy-puberulent. The margins of the blades are crispate-undulate, even in very young plants, although less so in these. The species is also characterized by its moderately long posterior lobes, usually narrowly rounded at the apex, and its matte, pale green petiole that is purple-speckled in transverse bands and sheathed about one half of its length, with the sheath erect and the margins inrolled. The most noteworthy distinction is the morphology of the synandria, which is rare in species from the eastern slopes, *C. engleri* being one of only five species from the eastern slopes with synandria more or less truncate at the apex. The ovaries of *C. engleri* are also distinctive in being (2)3- to 4-locular, a character found also in *C. cutucuensis* and in no other species from the eastern slopes. In spite of these similarities, the two species could not be confused.

Chlorospatha engleri could possibly be confused with *C. pubescens*, particularly in the sterile state,

which is widespread on the eastern slopes of the Andes in Ecuador, at 400–1400 m elevation (see discussion under *C. pubescens*). The leaf blades of *C. pubescens* are usually hastate to subhastate, velvety and broadly quilted on the upper surface, with only the midrib and major venation sunken. *Chlorospatha engleri* differs in having sagittate to weakly subhastate blades that are matte to matte-subvelvety and bullate on the upper surface.

Chlorospatha engleri could possibly be confused with *C. longipoda*, which is widespread on the eastern slopes of the Andes in Ecuador and occurs in the type locality of *C. engleri* (see discussion under *C. longipoda*). The shape of the blades of young plants of *C. engleri* is similar to that found in mature plants of *C. longipoda*. Mature leaf blades of *C. engleri* are usually somewhat triangular-sagittate, with the anterior lobe about 2.2 times longer than the posterior lobes, frequently less, and the upper surface bullate. Mature blades of *C. longipoda* are usually narrowly ovate-elliptic and subsagittate, with the anterior lobe usually 3.5 to 10 times longer than the posterior lobes and the upper surface usually quilted and never bullate. The margins of the blades are crispate-undulate in *C. engleri*, with the midrib and major venation weakly paler than the upper surface, finely ribbed and granular-puberulent on the lower surface, and in part sparsely crispy-puberulent, thus differing from *C. longipoda*, in which the margins are smooth and the venation concolorous on the upper surface and smooth and mostly glabrous on the lower surface.

A sterile collection, *Cerón et al.* 48869 (QAP), made in Parque Nacional Sangay, is possibly this species; however, all parts of the leaves are glabrous and the colliculate border along the veins is lacking.

24. *Chlorospatha feuersteiniae* (Croat & Bogner) Bogner & L. P. Hannon, comb. nov. Basionym: *Xanthosoma feuersteiniae* Croat & Bogner, Willdenowia 35: 327. 2005. TYPE: Ecuador. Morona-Santiago: along rd. from Patuca to Santiago through the S edge of the Cordillera de Cutucú, ca. 25 km E of Patuca, ca. 700 m, *Betsy Feuerstein in Croat* 84927 (MO) (holotype, MO!; isotypes, B!, K!, M!, QCNE!, S!, US!). Figures 24C, D, 46C.

Terrestrial herb, evergreen, glabrous; stems erect, 0.6–1.5 cm in diam.; internodes short. LEAVES erect-spreading, clustered near apex of stem; cataphylls 10–11 cm long, 0.8–0.9 cm wide, green with irregular purple markings and small rounded spots, acute and purple at apex; **petioles** 12–16.5 cm long, sheathed from about the middle of 2/3 of its length, medium green, heavily tinged purple toward apex,

weakly glossy; sheath broadly spreading 7–9.7 cm long, the margins somewhat membranaceous, more lightly colored, weakly reflexed, joining to form an acute and weakly free-ending (unfused) apex; free portion of petiole broadly and shallowly sulcate, the margins bluntly acute, 4 mm wide, 3 mm thick; **blades** narrowly ovate to lanceolate or somewhat elliptic, 15–20 cm long, 6.5–9.5 cm wide, 2 to 2.1 times longer than wide, distally tapered and \pm acute, ending abruptly with a mucro ca. 1 mm long, slightly cordulate to subcordate or truncate at base, subcoriaceous, dark green and semiglossy above, completely purple and slightly less glossy below, drying weakly glossy and yellow-green above, weakly glossy and purplish to medium yellow-green below; margins slightly undulate; major veins sunken and concolorous above, prominent and purplish below; midrib narrowly sunken above, thicker and slightly more purple than remaining lower surface; primary lateral veins in 4 to 6 pairs, narrowly rounded, arising at a very acute angle, then spreading at an angle of 35° – 40° , finally loop-connected along the margin; collective veins in 3 series, etched-sunken above, raised below, the innermost 4–10 mm from the margin, the second ca. 3 mm from the margin, the third antimarginal (ca. 1 mm from margin), all extending to near the apex; tertiary veins in part sunken above, raised below; reticulate veins somewhat prominulous below. INFLORESCENCE erect, usually solitary; peduncle 5.7–10 cm long, 0.2–0.4 cm wide, terete, medium yellow-green-tinged purple, matte; **spathe** 7–9 cm long, medium green in the lower 2–3 cm, then becoming whitish with the outer margins and apex purplish, not constricted but somewhat flattened above the pistillate zone; tube 2–3 cm long, 0.6–0.8 cm wide, medium yellow-green and matte outside, slightly paler and glossy within; limb 4.5–6 cm long, 0.8–1.5 cm wide, flattening to 3.5 cm wide, white toward apex with the margin purplish, \pm acute and hooked at apex; **spadix** 4–6 cm long, adnate at base for 0.8 cm shorter than spathe; pistillate zone cylindric, 1–1.5 cm long, 0.3–0.4 cm wide, creamy white; staminate zone 2.8–4 cm long, fertile to apex, white, terete and 0.35–5 mm in diam. or somewhat flattened, tapered toward apex; sterile zone 0.4–0.5 cm long, 0.25–0.3 cm wide, with 2 to 3 rows of synandrodies. Pistillate flowers densely arranged and without coherent styles; ovary ellipsoid, 1.2–1.3 mm long, 0.8–1.1 mm wide, pale green, usually with three deeply intrusive placentae, ovules several, hemianatropous; **stigma** disklike, 0.4–0.6 mm diam., darker green (drying brownish), \pm sessile, no broadened style present. Synandrodies densely arranged, 1.5–2 mm long, 0.8–1.4 mm wide, flattened

apically, sunken medially. Staminate flowers (synandria) \pm rounded, 1–1.1 mm high, 1–1.7 mm in diam., sunken in the center and incised between the thecae (as seen from above), the lowermost synandria elongate, 2 mm long and 1 mm wide, merging imperceptibly with the rounded synandria above (uppermost synandria sometimes sterile); thecae lateral, ca. 1 mm long, each opening by an apical pore, pores weakly depressed in the upper surface near the margin of the synandrium. Pollen 22 μ m long, 16–18(–22) μ m wide, ellipsoid to ellipsoid-oblong, in tetrads, exine reticulate.

Discussion. *Chlorospatha feuersteiniae* is known for certain only from the type locality in Morona Santiago in the Cordillera de Cutucú at ca. 700 m elevation, but the species has also been observed by Betsy Feuerstein in Zamora-Chinchipe in the Cordillera del Condor near Los Encuentros at ca. 760 m in premontane wet forest.

Croat and Bogner (2005) described *Xanthosoma feuersteiniae* before the “Revision of the genus *Chlorospatha*” by L. P. Hannon and T. Croat (available as a manuscript in early 2006) was completed. In February 2006, Lynn Hannon visited the Munich Botanical Garden, just a few months before she passed away, and the first author showed her the material of this species. It became clear that it represents a *Chlorospatha* species, and we agreed to publish the necessary new combination.

As Bogner and Gonçalves (2005) pointed out, the delimitation of the genera *Caladium*, *Xanthosoma*, and *Chlorospatha* becomes more and more difficult in light of the new material collected in recent decades. Two of the most distinguishing characters of pollen and gynoecium turned out not to be constant. According to Madison (1981), *Caladium* species release the pollen in monads and *Xanthosoma* in tetrads, but *X. mariae* Bogner & Gonçalves and *X. latestigmatum* Bogner & Gonçalves of *Xanthosoma* sect. *Acontias* shed the pollen in monads (see also Bogner & Gonçalves, 2005). On the other hand, *C. feuersteiniae* also has the pollen in tetrads as all species of this genus have, but furthermore its tetrads are very similar to those of *C. pubescens* Croat & L. P. Hannon, *C. ceronii* Croat & L. P. Hannon, and *C. hannoniae* Croat, all of which have a reticulate exine.

Concerning the gynoecium, *Xanthosoma* has usually been distinguished by the disklike, broadened, and coherent styles with a centrally smaller stigma. *Caladium* was distinguished by stigmas as broad as the ovary, often said to be sessile, but in fact there is a broad, unmodified style or stylar region present. Now we know at least five different types of styles in *Xanthosoma* (Gonçalves, 2004), and they are

not coherent in all cases. As it turned out, *C. feuersteiniae* has sessile stigmas, also known in the genus *Chlorospatha* (e.g., *C. longipoda* (K. Krause) Madison) and representing Hannon's style Type 1, but sessile stigmas are unknown in *Xanthosoma*. The unconstructed and apically hooked spathe of *C. feuersteiniae* is not like that in any species of *Xanthosoma* or *Chlorospatha*.

The synandrodies of *Chlorospatha* are usually free to partly or completely connate into irregular, fungiform, or lobed synandrodies and also truncate (prismatic) (e.g., *C. longipoda*) as is also the case in *C. feuersteiniae*. The latter also has truncate synandrodies with a length of ca. 2.5 mm, which are densely arranged in only two rows and sometimes have an incomplete third row. As far as we have observed, *C. feuersteiniae* only has a solitary inflorescence with a robust peduncle, while *C. longipoda* usually has several inflorescences with slender peduncles in a sympodium supported by the leaf sheath (very young plants have one inflorescence at first flowering, but some species are known with only one inflorescence).

25. *Chlorospatha gentryi* Grayum, Ann. Missouri Bot. Gard. 73: 468. 1986. TYPE: Colombia. Antioquia: trail from Encarnación to Parque Nac. Nat. Las Orquídeas, W slope of W Cordillera, 1600–1800 m, 27 Jan. 1979, A. Gentry & E. Rentería 24585 (holotype, MO-2715461!; isotypes, COL not seen, HUA-231692!). Figure 20A, B.

Terrestrial herb, to ca. 50 cm tall; stem erect, at least 10 cm tall, with remnants of old cataphylls persisting semi-intact at upper nodes, \pm fibrous, the fibers pale; internodes 1–2 cm long, drying 0.6–1.3 cm diam., dark reddish brown; cataphylls 6–15 cm long, obtuse with acumen at apex, 1-ribbed abaxially, drying \pm fibrous, matte to weakly glossy, tan to dark tan or medium-dark brown. LEAVES 2 to 7, erect-spreading; **petioles** 12–25 cm long, scurfy-pubescent in apical 1/4 to 1/2, usually more densely so near apex, drying weakly glossy, dark brown to occasionally almost black, sheathed 4–8 cm, ca. 1/4 to 1/3 of total length; sheath decurrent at apex; free portion drying 2–4(–5) mm diam. midway; **blades** 5- to 7-pedatisect or occasionally obscurely alate between segments, 13–22 \times 11–23 cm, about as wide as long, thin to thinly coriaceous (dry), bicolorous, the margins of all segments crispate-undulate; upper surface drying weakly glossy to semiglossy, dark brownish green; lower surface reticulate, drying weakly glossy to semiglossy, weakly to moderately paler, rarely concolorous; all segments \pm acute at base, with margins straight to attenuate toward the

base, occasionally cuneate; **medial lobe** elliptical, 6.5–15.5 \times 2.5–6.8 cm, 2.3 to 2.8 times longer than wide, 1.1 to 3.9 times longer than lateral lobes, acuminate at apex, occasionally equal in length to or weakly shorter than innermost lateral lobes, broadest midway, \pm symmetrical, usually free to the base, rarely narrowly attached and weakly confluent with innermost lateral lobes, the confluent portion ca. 1 mm wide; **lateral lobes** (2–)4.5–15 \times (1–)1.2–6 cm, 2.2 to 3.7 times longer than wide, acuminate at apex, occasionally acute on outermost 1 to 2 segments (rarely bluntly acute), broadest at or below middle (rarely above middle), progressively shorter and narrower toward outermost segments, the outermost much shorter than innermost; sides (of lateral lobes) moderately progressively inequilateral toward outermost segments, the inner side always narrower; outer side 1.5 to 2.1 times wider than inner side midway; all orders of venation crispy-puberulent and raised or prominulous on lower surface; midrib round-raised on lower surface, drying raised to weakly flattened, moderately darker than surface; posterior rib naked 1.2–3.5 cm per side, densely scurfy-pubescent; primary lateral veins on all segments (3)4 to 6 pairs, arising at 25°–40°, straight to weakly arcuate, drying weakly raised to \pm flattened on lower surface, weakly to moderately darker than surface; secondary veins drying weakly raised on lower surface, weakly darker than surface; tertiary veins drying weakly raised or prominulous on lower surface, weakly darker than surface; reticulate veins drying in part prominulous, otherwise flat on lower surface, concolorous to weakly darker than surface; collective veins 3, the innermost arising from lowermost lateral vein at base, loop-connected with all preceding lateral veins, occasionally markedly scalloped, remote from margin, 3–15 mm from margin. INFLORESCENCES erect, 2 to 3 per axil; peduncle held within the sheath, 6.5–10 cm \times 1–1.5 mm (dry), \pm crispy-puberulent, most densely so near apex, drying matte to weakly glossy, blackish brown; **spathe** erect, ca. 4.2 cm long, cuspidate at apex; spathe tube green, greenish or whitish, densely crispy-puberulent on outer surface, white on inner surface, 2–2.5 cm \times 3.5–5 mm, drying matte to weakly glossy, dark blackish brown on both surfaces, densely cream, punctiform on inner surface; spathe blade whitish or yellow, 2–2.4 cm \times 3–3.5 mm, narrowly crispy-puberulent along the veins toward base abaxially, drying weakly glossy, dark tan to dark brown on outer surface, semiglossy on inner surface, opening broadly at anthesis, marcescent, erect after anthesis; **spadix** erect, ca. 3.8 cm long, sessile, adnate to spathe 0.7–1 cm at base, ca. 1/2 of the length of pistillate portion; pistillate portion



Figure 20. A, B. *Chlorospatha gentryi* Grayum, the type *Gentry & Rentería* 24585 (MO). —A. Herbarium isotype (COL-231692). —B. Plant with three inflorescences, with the one at far left (paler spathe) in full anthesis. —C. *Chlorospatha giraldoi* Croat & L. P. Hannon, the paratype specimen *W. Vargas* 5363 (COL-125515). —D. *Chlorospatha grayumii* Croat & L. P. Hannon, the holotype *Killip* 35298 (US-1772027).

1.2–2.2 cm long, drying 2.5–3.5 mm diam., broadest midway, medium reddish brown to dark brown; fertile staminate portion green, ca. 1.4 cm long, drying ca. 2 mm diam., narrowly rounded at apex, cylindrical, weakly pink-tinged medium brown; sterile staminate portion ca. 6 mm long, drying 1–1.75 mm diam., broadest at apex, pale to medium yellowish tan, the axis bare 1–1.5 mm at base; pistils \pm weakly coherent, 3 to 4 across the axis (viewed from above), 1–1.2 mm long; ovaries subglobose, 1.5–2 mm diam., drying tan; style Type 3 (Fig. 1), drying 0.3–0.5 mm diam., narrower than ovary apex, the margins not coherent with those of adjacent styles; **stigma** ca. 0.1–0.3 mm diam., sessile, disklike, truncate at apex, drying medium reddish brown to dark blackish brown; synandria ca. 1×1 –1.3 mm, deeply (2)3- to 4-lobed, (2)3- to 4-androus, coherent, truncate; sterile flowers drying ca. 0.5 (or less) \times ca. 1 mm, weakly elongated in direction of axis, coherent, truncate, \pm prismatic, in 4 to 5 whorls. **INFRUCTESCENCE** green, drying 2.5–4.2 cm \times 5–8 mm, weakly glossy, dark brown to blackish brown; berries green, drying 2–5 mm diam.

Phenology. Flowering is only known to occur in *Chlorospatha gentryi* during January and December, with fruiting recorded for December.

Discussion. *Chlorospatha gentryi* is known only from the Parque Nacional Natural Las Orquídeas in Antioquia Department, Colombia, in what is possibly either premontane rain forest or tropical wet forest on the western slopes of the Cordillera Occidental, at 1200–1800 m elevation.

Chlorospatha gentryi, a member of *Chlorospatha* sect. *Chlorospatha*, is a small, erect-growing plant distinguished by its 5- to 7-pedatisect leaf blades with the segments acute at the base and crispate-undulate along the margins, and all abaxial venation more or less raised and crispy-puberulent. The petiole is scurfy-pubescent for one fourth to one half of its length, prominently so toward the apex and onto the posterior rib. The inflorescence of *C. gentryi* is unusually small, with the spathe 4.2 cm long and the peduncle short (to 10 cm long) and crispy-puberulent, with the indumentum extending onto the outer surface of the spathe tube and narrowly onto the blade. The innermost collective vein is noteworthy in being markedly scalloped and remote from the margin, relative to the size of the segments. The species is also distinguished by its green synandria.

Chlorospatha gentryi could be confused with only one species, *C. morae* from the western slopes of the Cordillera Occidental in Chocó Department, Colombia, at 285–825 m elevation (see discussion under *C.*

morae). The latter species is a larger plant with the stem erect to 50 cm, occasionally nine segments on the blades (vs. five to seven in *C. gentryi*), longer peduncles, and larger inflorescences. The petiole of *C. morae* is sheathed about one half of its length, with both it and the midrib glabrous and finely striate-ridged, differing from *C. gentryi* in which the petiole is sheathed one fourth to one third of its length and partially pubescent, as is the midrib, with neither structure striate-ridged. Mature blades of *C. morae* have six to seven or as many as eight or nine pairs of primary lateral veins on all but the outermost segments, thus differing from those of *C. gentryi*, which have no more than four to six pairs.

The synandria of *Chlorospatha gentryi* appear to be unusual, at least in dried material. The lobes are conspicuously deeply divided, each appearing to be quite separate from the other, with the two pores on each lobe separated by a considerable distance, a condition also observed in *C. engleri*, known only from the eastern slopes of the Andes.

Additional specimens examined. COLOMBIA. **Antioquia:** Mpio. Frontino–Mpio. Urrao, Parque Nac. Nat. Las Orquídeas, Calles–Carauta rd., *Callejas et al.* 3086 (HUA, MEDEL, MO, NY); Mpio. Urrao, Parque Nac. Nat. Las Orquídeas, vic. Calles, rt. side of Río Calles, *Pipoly et al.* 17803 (JAUM, MO).

26. *Chlorospatha giraldoi* Croat & L. P. Hannon, sp. nov. TYPE: Colombia. Valle: Finca Zigara, Km. 18 on Calí–Buenaventura Hwy., Km. 4 via Dapa, Elvira distr., 1900 m, 3°30'N, 76°34'W, 13 Mar. 1994, *J. Giraldo & L. Agredo* 228 (holotype, MO-05071722!; isotypes, CUVC not seen, TULV not seen). Figure 20C.

Herba usque ad ca. 2 m, plerumque terrestres; internodia (1.5–)2–3.5 \times 1–2.5 cm; cataphylla (15–)32–37 cm longa. Petiolus (41–)45–74 cm longus, vaginatus per (18–)38–39 cm; lamina foliaris subhastata, (18.5–)23–35.5 \times (16.5–)21–25 cm, lobis posterioribus 11–14.5 \times 2.5–5 cm, nervis basalibus utroque ca. 6, nervis primariis lateralibus utroque (5)6. Inflorescentiae usque ad 5 in quaque axilla; pedunculus (23–)25–38 cm \times 2–4 mm; spatha erecta, (9.5–)11–13 cm longa, tubo (4.5–)5–7.8 cm \times 4–5 mm, lamina 5–6 cm \times ca. 5 mm; spadix (8.5–)9.5–10 cm longus.

Terrestrial or hemiepiphytic herb, to ca. 2 m tall (probably only when hemiepiphytic); stem decumbent, with remnants of old leaf bases and cataphylls persisting \pm intact along its length; internodes (1.5–)2–3.5 \times 1–2.5 cm, drying weakly glossy, medium-dark to dark brown, occasionally gray-tinged (all measurements made from dried material); cataphylls (15–)32–37 cm long, acuminate or cuspidate at apex, drying weakly glossy to semiglossy, dark reddish brown. LEAVES 2 to 3, erect-spreading; **petioles**

(41–)45–74 cm long, drying glabrous, weakly glossy to semiglossy, dark brown, sheathed (18–)38–39 cm, ca. 2/3 of total length or slightly less; sheath decurrent at apex; free portion 3–4 mm diam. midway; **blades** subhastate, occasionally sagittate in juvenile plants, (18.5–)23–35.5 × (16.5–)21–25 cm, 1.1 to 1.4 times longer than wide, weakly to abruptly acuminate at apex, broadest at base, 2.1 to 2.8 times wider at base than across anterior lobe (measured tip to tip across posterior lobes), occasionally weakly to strongly constricted on one side in area of petiole attachment, thin, drying weakly bicolorous to concolorous; upper surface matte, dark green, drying matte, dark brown; lower surface semiglossy, drying weakly glossy to semiglossy, rarely in part weakly olive-tinged (in young plants); anterior lobe (11.5–)15–24.5 × (6.5–)7.6–10 cm, 1.7 to 2.5 times longer than wide, (1 to)1.2 to 1.6 times longer than posterior lobes, broadest at or below middle, ± symmetrical; posterior lobes directed somewhat outward, 11–14.5 × 2.5–5 cm, (3 to)3.5 to 5 times longer than wide, acute to bluntly acute at apex, broadest at or near base, ± symmetrical, the inner side ± rounded toward base, usually briefly attenuate onto petiole apex; outer side weakly concave toward base; midrib round-raised on lower surface, drying raised and weakly flattened, weakly darker than surface; **basal veins** ca. 6 pairs, coalesced into a prominent posterior rib; posterior rib rarely naked 5–10 mm per side (Vargas 5363); primary lateral veins (5)6 pairs, arising irregularly at 40°–75°, weakly or strongly arcuate to irregularly ascending, raised on lower surface, drying ± flattened, weakly darker than surface; secondary veins raised on lower surface, drying weakly prominulous, weakly darker than surface; tertiary veins drying visible and distinct on lower surface, weakly darker than surface; reticulate veins drying obscure; collective veins 3, the innermost arising from one of the lowermost lateral veins on inner side of posterior lobe, loop-connected with all preceding lateral veins, ± parallel to and 2.5–6 mm from margin. INFLORESCENCES erect, to 5 per axil; peduncle held within the sheath, (23–)25–38 cm × 2–4 mm, drying weakly glossy to semiglossy, pale-medium to dark brown; **spathe** erect, creamy yellow or yellowish white, (9.5–)11–13 cm long, cuspidate at apex; spathe tube (4.5–)5–7.8 cm × 4–5 mm, drying weakly glossy, medium-dark to dark brown on outer surface, weakly glossy on inner surface; spathe blade 5–6 cm × ca. 5 mm, drying matte to weakly glossy, medium reddish brown on both surfaces, marcescent, erect after anthesis; **spadix** erect, (8.5–)9.5–10 cm long, sessile, adnate to spathe 4–5.5 cm at base, the entire length of

pistillate portion; pistillate portion 4–5.5 cm × 2–3 mm, drying dark, reddish brown; fertile staminate portion creamy yellow, 2.5–3.7 cm × 2–5 mm, narrowly rounded to bluntly acute at apex, ellipsoid, drying pale-medium brownish yellow to medium-dark yellowish brown; sterile staminate portion (1.2–)1.4–1.8 cm × 1.5–3 mm, ± cylindrical, drying dark reddish brown; pistils ± laxly arranged, 2 to 3 across the axis (viewed from above), 1.8–2 mm long; ovaries subglobose, ca. 1 × 1.5–2.2 mm, drying pale tan to brownish cream; style Type 8 (Fig. 1), 0.8–1 × 1.5–2 mm, comprising ca. 1/2 of the length of pistil, the margins possibly weakly coherent with those of adjacent styles (in living material); **stigma** prominent, 0.5–0.9 mm diam., prominently elevated on and broader than narrowed portion of style, drying tan to dark reddish brown; synandria ca. 1 × 1.5–2 mm, coherent, truncate, 3- to 4(5)-lobed, 3- to 4(5)-androus; sterile flowers ca. 1 mm long, 0.5–2.5 × 0.5–1 mm diam. and ± elongated in direction of axis, or 0.5–1 mm diam. and deeply irregularly lobed in apical 1 to 2 whorls, otherwise 1- to 5-branched, the branches 0.6–1 mm long, broadest and obtusely truncate at apex, abruptly and weakly narrowed toward base, ± densely arranged in 8 to 10 whorls. Berries not known.

Phenology. Flowering is only known to occur in *Chlorospatha giraldoi* during the months of March and December.

Etymology. *Chlorospatha giraldoi* is named for Jorge Giraldo Gensini, Colombian botanist and one of the collectors of the type.

Discussion. *Chlorospatha giraldoi* is known only from tropical wet forest and what is either premontane wet forest or lower montane wet forest to the north and northwest of Calí, along the Continental Divide, on both the eastern and western slopes of the Cordillera Occidental in Valle Department, Colombia, at 1700–2000 m elevation. The species would be expected to occur elsewhere in the department.

Chlorospatha giraldoi is a member of *Chlorospatha* sect. *Occidentales* and is distinguished by its frequently hemiepiphytic habit and matte, dark green, subhastate leaf blades that dry dark brown and weakly or not at all bicolorous, with the posterior lobes narrow and long, relative to the length of the anterior lobe, the latter being only 1.2 to 1.6 times longer than the posterior lobes. The species is also distinguished by its large inflorescence (11–13 cm long), with the spathe entirely creamy yellow or yellowish white, the fertile staminate portion of the spadix creamy yellow and the sterile staminate

portion long (1.3–1.8 cm long), with most of the sterile flowers 1- to 5-branched. The long-attenuated style (Type 8, Fig. 1), with the mantle appressed to the ovary, is uncommon in the genus.

Chlorospatha giraldoi could be easily confused with *C. noramurphyae*, also from the vicinity of Cali on the eastern slopes of the Cordillera Occidental, and is possibly sympatric with that species (see discussion under *C. noramurphyae*). The two species are quite similar in certain respects, both having subhastate leaf blades with narrow posterior lobes and large inflorescences with similar styles and sterile flowers, but differ in significant ways. The species are probably closely related and might eventually prove to be conspecific.

Chlorospatha giraldoi could possibly be confused with *C. ricaurtensis* from Reserva La Planada on the western slopes to the south, in Nariño Department, along the border with Ecuador, at 1800 m elevation (see discussion under *C. ricaurtensis*). *Chlorospatha ricaurtensis* has sagittate blades that dry semiglossy and greenish on both surfaces, with three pairs of primary lateral veins and the posterior lobes directed toward the base. *Chlorospatha giraldoi* differs in having subhastate leaf blades that dry dark brown on both surfaces, matte on the upper surface, with six pairs of primary lateral veins.

Paratypes. COLOMBIA. **Valle:** vic. Dapa, NW of Cali, along Continental Divide, 2000 m, *Croat 61433* (MO); Mpio. La Cumbre, Bitaco region, Res. Agua Bonita, 1700–1900 m, 10–15 Dec. 1998, *W. Vargas 5363* (COL-125515, HUA, MO).

27. *Chlorospatha grayumii* Croat & L. P. Hannon, sp. nov. TYPE: Colombia. Chocó: Corcovada region, upper Río San Juan, ridge along Yeracüí Valley, 200–275 m, 24–25 Apr. 1939, *E. Killip 35298* (holotype, US-1772027!). Figure 20D.

Herba hemiepiphytica vel terrestris, usque ad plus quam 50 cm; internodia 1–1.5 × 1–1.3 cm; cataphylla 8–23 cm longa. Petiolus 29–61 cm longus; lamina foliaris oblongo-elliptica, sagittata, 38–62 × 9.5–23 cm, lobis posterioribus 11.5–19.5 × 3–7 cm, nervis basalibus utroque 3 vel 4, nervis primariis lateralibus utroque 6 ad 9. Inflorescentia 1 in quaque axilla; pedunculus ca. 23 cm × 2–3 mm; spatha erecta, tubo ca. 2.6 cm × 5 mm; spadix erectus, ca. 4.2 cm longus.

Hemiepiphytic or terrestrial herb, slightly more than 50 cm tall; stem erect or decumbent, with remnants of old cataphylls persisting ± intact along its length and weakly fibrous; internodes 1–1.5 × 1–1.3 cm, drying weakly glossy, dark brown (all measurements made from dried material); cataphylls 8–23 cm long, cuspidate or obtuse with acumen at

apex, 1-ribbed abaxially, drying matte to weakly glossy or semiglossy, medium-dark to dark reddish brown or blackish brown, weakly fibrous. LEAVES 2, probably erect-spreading; **petioles** 29–61 cm long, drying glabrous, matte to weakly glossy, dark reddish or blackish brown, occasionally semiglossy, sheathed 13–25 cm, ca. 1/3 of total length; sheath free-ending at apex (decurrent when sterile); free portion 3.5–8(–10) mm diam. midway, D-shaped, with low medial keel, the margins ± acute; **blades** oblong-elliptic, sagittate, 38–62 × 9.5–23 cm, 2.6 to 4 times longer than wide, briefly to abruptly acuminate at apex, rarely gradually acuminate, as broad as or weakly broader at base than across anterior lobe (measured tip to tip across posterior lobes), weakly to prominently constricted in area of petiole attachment, thinly coriaceous, weakly bicolorous; upper surface semiglossy, green, drying matte to semiglossy, medium greenish brown or blackish brown; lower surface semiglossy, drying weakly glossy to semiglossy or occasionally glossy, concolorous to weakly paler, with blotchlike, diffuse punctations (30×); anterior lobe 26–48 × 9.5–18.5 cm, 2.6 to 2.9 times longer than wide, 2.2 to 4.4 times longer than posterior lobes, broadest near base, ± symmetrical to weakly inequilateral; posterior lobes directed toward the base, occasionally weakly outward, 11.5–19.5 × 3–7 cm, (2.4 to) 3.1 to 4.3 times longer than wide, narrowly rounded at apex or rarely weakly acuminate with the tip narrowly rounded, broadest at base, weakly inequilateral, the inner side narrower, rounded toward base, briefly attenuate and weakly confluent with opposite lobe at base, the confluent portion obscuring petiole apex; outer side 1.2 to 2.2 times wider than inner side midway; midrib and major veins sunken on upper surface, convex on lower surface, granular-puberulent, drying ± flattened, moderately to prominently darker than surface; **basal veins** 3 to 4 pairs, coalesced into a prominent posterior rib; primary lateral veins 6 to 9 pairs, arising at 30°–55°, most acutely toward apex, moderately to prominently arcuate; secondary veins raised on lower surface, granular-puberulent, drying raised, weakly to moderately darker than surface; tertiary veins raised on lower surface, drying in part prominulous, otherwise visible, concolorous to weakly darker than surface; reticulate veins drying in part visible or ± obscure on lower surface, ± concolorous; collective veins 3 to 4, the innermost arising from one of the lowermost lateral veins on inner side of posterior lobe, ± parallel to and 3–8 mm from margin. INFLORESCENCE erect, 1 per axil; peduncle held within the sheath, 23 cm × 2–3 mm, narrowest toward base, drying weakly glossy, pale

tan; **spathe** erect (total length not known); spathe tube $2.6 \text{ cm} \times 5 \text{ mm}$, drying matte, medium brown on outer surface, moderately paler on inner surface; spathe blade (total length not known) drying moderately paler than tube; **spadix** erect, 4.2 cm long, sessile, adnate to spathe ca. 1.7 cm at base, most of the length of pistillate portion; pistillate portion $1.9 \text{ cm} \times 3.5 \text{ mm}$, drying orangish tan; fertile staminate portion $2 \text{ cm} \times 4\text{--}5 \text{ mm}$, narrowly rounded at apex, ellipsoid, drying dark reddish brown; sterile staminate portion ca. $1 \text{ cm} \times 1.5\text{--}3 \text{ mm}$, broadest at apex, drying dark purplish brown; pistils weakly coherent, 3 to 4 across the axis (viewed from above), 1–2 mm long; ovaries subglobose, 1.5–2 mm diam., drying cream to pale tan; style Type 5 (Fig. 1), ca. $1 \times 1.5\text{--}2 \text{ mm}$, broader than ovary apex, the margins (probably) weakly coherent with those of adjacent styles; **stigma** ca. 0.3 mm diam., elevated on and weakly broader than narrowed portion of style; synandria ca. $1 \times \text{ca. } 1 \text{ mm}$, coherent, truncate, 2- to 4-lobed, 2- to 4-androus (mostly 3); sterile flowers $0.5\text{--}1 \times 0.7\text{--}1 \text{ mm}$, coherent in apical 3 whorls, markedly laxly arranged in basal 3 whorls (axis mostly bare), truncate, subprismatic, in 6 whorls. Berries not known.

Phenology. Flowering is only known to occur in *Chlorospatha grayumii* during the month of April.

Etymology. *Chlorospatha grayumii* is named for Michael Grayum (1949–), author of several taxa of *Chlorospatha* and one of the first modern suprageneric phylogenies of the Araceae, authority on aroid pollen and the aroid flora of Costa Rica.

Discussion. *Chlorospatha grayumii* is known from three collections made in tropical wet forest and tropical rainforest on the western slopes of the Cordillera Occidental in Colombia, in Cauca and Chocó departments, at 90–275 m elevation. The type, the only fertile collection, was collected in 1939, in the Corcovada region of the upper Río San Juan in Chocó, at 200–275 m elevation. Corcovada could not be located on current maps, and it is possible that it no longer exists as a place name. Given the elevation, the type locality is possibly in the area of Quebrada Antón, south of the road between Tado and Santa Cecilia. A second collection was made south of Quibdó, along the road to Istmina, at 90 m elevation. One collection was made near the coast, at Timbiquí, the only collection from Cauca. The species would be expected to occur in other areas within Cauca and Chocó, at similar elevations.

Chlorospatha grayumii is a member of *Chlorospatha* sect. *Occidentales* and is distinguished by its

narrowly sagittate, oblong-elliptic leaf blades that are occasionally as long as or slightly longer than the petioles, with the posterior lobes narrow and the anterior lobe more than twice as long as the posterior lobes, occasionally as much as 4.4 times longer. The inner sides of the posterior lobes are narrowly confluent at the base, obscuring the petiole apex, an unusual condition in *Chlorospatha*. The species is also distinguished by its small inflorescence with the spadix only 4.2 cm long.

Chlorospatha grayumii could be confused with only one species, *C. longiloba*, from the western slopes of the Andes in northern Ecuador near the Colombian border at 300–800 m elevation. The petiole of *C. longiloba* is sheathed one half of its length, with the sheath decurrent at the apex and inflorescences emerging from a sympodial cataphyll at the base of the sheath, thus differing from *C. grayumii*, wherein the petiole is sheathed one third of its length, with the sheath free-ending and inflorescences emerging from the apex of the sheath. The free portion of the petiole is sharply D-shaped, with a low medial keel in the latter species, and terete or subterete in *C. longiloba*. In *C. longiloba*, the spadix is adnate to the spathe one half of the length of the pistillate portion, with the fertile staminate portion tapering and broadest at the base, whereas that of *C. grayumii* is adnate almost the entire length of that portion, with the fertile portion ellipsoid. Madison (1981) originally filed the type for *C. grayumii* as *C. lehmannii* (see discussion under *C. lehmannii*).

Paratypes. COLOMBIA. **Cauca:** Timbiquí, 100 m (est.), 1903, *C. Lehmann* 390A (K). **Chocó:** ca. 15 km S of Quibdó on rd. to Istmina (Pan-American Hwy.) & 8–10 km E on rd. to petroleum exploration camp, 90 m, $5^{\circ}35'N$, $76^{\circ}37'W$, 9 July 1986, *M. Grayum*, *B. Hammel*, *J. Kress* & *G. Brown* 7647 (HUA, MO).

28. *Chlorospatha hammeliana* Grayum & Croat, *Ann. Missouri Bot. Gard.* 73: 466–467. 1986. TYPE: Panama. Coclé: just N of sawmill above El Copé, Atlantic slope, ca. 1000 m, 25 Aug. 1983, *B. Hammel* & *J. Kress* 13465 (holotype, MO-3340241!; isotype, DUKE!). Figures 4A, 21A–D.

Terrestrial herb, to ca. 1 m tall; stem erect, 5–20 cm tall, with remnants of old cataphylls persisting semi-intact, covering the stem, weakly fibrous, the fibers pale; sap milky; internodes $1\text{--}2 \times 1\text{--}3 \text{ cm}$, scurfy, brown, drying 1–1.5 cm diam., matte, dark brown; cataphylls 10–18 cm long, obtuse with acumen at apex (acumen 5–10 mm long), 1-ribbed abaxially, drying weakly fibrous, matte to weakly glossy, dark reddish brown on outer surface, weakly



Figure 21. *Chlorospatha hammeliana* Grayum & Croat. —A. Leaf blade adaxial surface, with simple ovate-cordate blade, photo of MO cultivar from Croat 75071. —B. Leaf blade adaxial surface, with two constricted posterior lobes, this condition intermediate to the simple and 3-lobed leaves and variable within collections attributed to this species, from Croat 44589 (MO). —C. Leaf blade adaxial surface, with 3-lobed blade, from Croat & Zhu 76881 (MO). —D. Inflorescence at anthesis, from Croat 44589 (MO).

to moderately paler on inner surface. LEAVES 1 to 3, erect-spreading; **petioles** (21–)26–70 cm long, spongy to moderately firm, glabrous, semiglossy, entirely medium to dark green, violet-purple or purple-tinged green, or green to medium yellow-green and violet-purple– or dark purple–mottled, drying matte to weakly glossy, medium-dark to dark reddish brown, frequently with the epidermis in part weakly separated \pm intact and semiglossy, sheathed 6.5–15.5 cm, 1/6 to 1/4(to 1/3) of total length; sheath decurrent at apex; free portion 3–7(–15) mm diam. midway (dry), terete or subterete; **blades** simple, ovate and cordate, or sagittate, subhastate or sub-3-lobed (rarely 3-lobed), (21–)25–44 \times (13.2–)16–40(–43) cm, (1)1.1 to 1.7(to 2) times longer than wide (2 times wider than long when 3-lobed), briefly or abruptly acuminate at apex, as broad as or weakly to prominently narrower or wider at base than across anterior lobe (measured tip to tip across posterior lobes), (1 to)1.3 to 1.6(to 1.9) times wider at base, or 1.5 to 2 times wider across anterior lobe than at base, weakly to prominently or not at all constricted in area of petiole attachment, the constriction 1.5–8.5 cm narrower than anterior (or medial) lobe, subcoriaceous, conspicuously bicolorous, drying thinly coriaceous, moderately to conspicuously bicolorous; upper surface \pm flat or weakly to moderately quilted, semiglossy to glossy, dark green, drying matte to semiglossy, dark green, olive-green or occasionally brownish; lower surface semiglossy, drying semiglossy to glossy, green to gray-tinged or yellow-tinged green; anterior lobe (17.2–)18–30.5(–35) \times (13.2–)16–27(–31) cm, (1)1.1 to 1.5 times longer than wide, (1.2)1.3 to 3.5(to 3.8) times longer than posterior lobes, broadest below middle, rarely midway, weakly to prominently or not at all constricted at base, \pm symmetrical; **medial lobe** (when present) 27.5 \times 22.5 cm, 1.2 times longer than wide, 1.3 times longer than lateral lobes, abruptly acuminate at apex, broadly attached at base, 5 cm wide at point of attachment, \pm symmetrical; posterior lobes directed toward the base or weakly to moderately outward, (3.8–)5–17.5(–21) \times 5–15.5(–17.5) cm, (1 to)1.2 to 2.3 times longer than wide, broadly rounded, acute to bluntly acute or rarely narrowly rounded at apex, broadest at base or below middle, \pm symmetrical or moderately inequilateral, the outer side narrower; inner side (1 to)2 to 2.5 times wider than outer side midway, \pm acute to truncate at base; **lateral lobes** (when present) directed toward the apex, 21–22.2 \times 11.2–11.5 cm, 1.8 to 2 times longer than wide, weakly briefly acuminate at apex, broadest at or below middle, moderately inequilateral, the inner side narrower, \pm acute toward base, narrowly confluent with medial

lobe, the confluent portion 5–6 mm wide; outer side 2.4 to 2.7 times wider than inner side midway; midrib and major veins convex, dark green on lower surface, drying \pm flattened, conspicuously to occasionally moderately darker than surface, frequently blackish; midrib weakly to moderately sunken on upper surface, rarely paler than surface; **basal veins** 4 to 9 branching off, weakly coalesced into a short posterior rib, first 1 to 5 fused at the base, 2 to 4 acroscopic, 2 to 5 basiscopic, or with 3 to 4 pairs coalesced into a prominent posterior rib; posterior rib naked 0.5–1.5 cm per side or not at all (naked 8 mm per side when 3-lobed); primary lateral veins (of medial or anterior lobe) 3 to 4 pairs, arising at 20°–65°(–75°), most acutely toward apex, \pm straight to weakly arcuate, weakly to moderately sunken or weakly depressed on upper surface; primary lateral veins (on lateral lobes, when present) 4 pairs, aggregated toward base, arising in basal 1/3, weakly to moderately arcuate; secondary veins sunken or flat on upper surface, raised on lower surface, darker than surface, drying entirely or in part weakly raised and otherwise visibly distinct, moderately darker than surface; tertiary veins occasionally weakly sunken or etched on upper surface, obscure to occasionally weakly etched on lower surface, occasionally darker than surface, drying entirely obscure and concolorous, or in part visibly distinct and otherwise obscure; reticulate veins drying obscure; collective veins 3, the innermost arising from base or one of the lowermost lateral veins on inner side of posterior lobe (outer side on lateral lobes), loop-connected with all preceding lateral veins, moderately to markedly scalloped, markedly remote and ca. 0.8–2.3(–2.8) cm from margin. INFLORESCENCES erect to erect-spreading, 2 to 3 per axil; peduncle held within the sheath only toward the base, 23.7–40 cm \times ca. 5 mm, terete, \pm spongy, green, drying weakly glossy, dark brown; **spathe** curved forward, 8.5–12 cm long, 3.6–4.5 cm wide in lower 1/3 (flattened), to 4 cm longer than spadix, lanceolate, cuspidate or abruptly acuminate at apex; spathe tube matte, green or greenish on outer surface, semiglossy, purplish or green on inner surface, 3.5–5.5 cm \times ca. 7 mm (dry), drying matte, dark brown on outer surface, weakly glossy to semiglossy and weakly to moderately paler on inner surface; spathe blade matte, white or greenish white on outer surface, semiglossy on inner surface, 5–6.5 cm long, 2–3.5 cm wide (flattened), drying matte, dark tan on outer surface, weakly glossy on inner surface, opening narrowly at anthesis, marcescent, erect after anthesis; **spadix** 5.7–7.5 cm long, sessile, adnate to spathe ca. 6–8 mm at base, 1/4 to 1/3 of the length of pistillate portion; pistillate portion greenish

white, 2.4–3.5 cm long, drying 3–5.5 mm diam., \pm cylindrical, pale yellowish to purplish; fertile staminate portion white or cream, 1.6–2 cm long, weakly clavate or tapering, narrowly rounded to bluntly acute at apex, drying ca. 5 mm diam., dark brown to weakly purplish brown; sterile staminate portion white or whitish, (1–)1.4–2.2 cm long, usually with axis naked 1–3 mm at base, drying ca. 5 mm diam., pale yellowish tan to yellowish cream, with reddish chromoplasts; pistils weakly coherent, 4 to 6 across the axis (viewed from above), 1.6–2.2 mm long; ovaries greenish white, \pm conical to cylindrical, 1.3–1.8 mm diam., drying whitish; style Type 3 (Fig. 1), as broad as or weakly narrower than ovary apex, the margins not coherent with those of adjacent styles; **stigma** yellowish, 0.3–0.5 mm diam., sessile, disklike, obtusely truncate at apex; synandria ca. 1 \times ca. 1 mm, coherent, truncate, deeply 3- to 5-lobed, 3- to 5-androus (mostly 4); pollen (from Grayum, 1986) in planar tetrads, inaperturate, minutely rugulate or verruculate, the individual grains 23–25 μ m (mean, 24 μ m) diam., starchless, binucleate; sterile flowers 1–1.2 \times 0.7–2.2 mm, \pm laxly arranged to weakly coherent, irregularly deeply 4- to 6-lobed, usually (1)2- to 4-branched in basal 1 to 2 whorls, in 5 to 7 whorls. Berries not known.

Phenology. Flowering is known in *Chlorospatha hammeliana* from one wild collection made on 25 August. The live voucher of a sterile collection (Croat 44589) later flowered in cultivation on 13 August.

Discussion. *Chlorospatha hammeliana* is known from two geographically isolated areas along the Continental Divide in west-central Panama: in the area of the sawmill above El Copé in Coclé Province on the Atlantic slopes at 710 to ca. 1000 m elevation, in lower montane wet forest and premontane rainforest; and in the vicinity of Santa Fé on the slopes of Cerro Tute in Veraguas Province. Three sterile collections were made in the latter area, two in premontane rainforest and premontane wet forest on the Pacific slopes at 800–1150 m elevation, and one in lower montane rainforest on the Atlantic slopes at 700 m elevation. The species is one of only two species in *Chlorospatha* sect. *Chlorospatha* that can usually or occasionally have other than divided blades. There are notable differences in the vegetative parts of the collections made in Coclé and those made in Veraguas, the most significant being the prominently 3-lobed leaf blade of one specimen of a collection from Veraguas (Croat & Zhu 76881, seen in Fig. 21C), the second specimen of the same collection having an ovate-cordate blade similar to the typical collections from Coclé. The other two collections from Veraguas exhibit a condition interme-

diate between the 3-lobed blade and the simple blade of the Coclé collections, having the blades prominently constricted in the area of petiole attachment (approaching the 3-lobed condition, as in Fig. 21C), with the posterior lobes narrow (2 to 2.3 times longer than wide), well-developed, and acute to weakly acuminate at the apex. The constriction is almost half as wide as the anterior lobe. The above suggests the possibility that more mature plants might eventually develop 3-lobed blades, as seen in Croat & Zhu 76881 (Fig. 21B). Some blades of the Coclé collections are sagittate to subhastate at the base and moderately constricted in the area of petiole attachment, but with the constriction weak or less prominent, more than three fourths as wide as the anterior lobe. These also have well-developed posterior lobes, but the lobes are broad, 1 to 1.5 times longer than wide, and broadly rounded at the apex. The petioles of the Coclé collections are entirely green, whereas those of the Veraguas collections are purple-violet, purple-tinged, or green with purple-violet or dark purple mottling. It is unfortunate that all three of the Veraguas collections are sterile and that floral characters could not be compared, but in all other respects, these collections accord well with both living and dried material from Coclé. However, it is possible that the collections from these two areas represent different taxa.

The typical form of *Chlorospatha hammeliana* is distinguished by its semiglossy, dark green petiole, sheathed one sixth to one fourth of its length, and subcoriaceous, semiglossy to glossy, conspicuously bicolorous leaf blades that are simple, ovate to sagittate, cordate at the base, and weakly or not at all constricted in the area of petiole attachment, with the major venation dark green on the lower surface. The species is also distinguished by the unusually long sterile staminate spadix (1.4–2.2 cm long), frequently longer than the fertile staminate portion, with the sterile flowers more or less laxly arranged and deeply irregularly 4- to 6-lobed or occasionally branched in the basal one or two whorls. The typical form could not be confused with any other taxon.

The 3-lobed specimen of *Chlorospatha hammeliana* is remarkably similar to *C. mirabilis*, a primarily Colombian species that has been collected in sterile condition in southern Darién Province, Panama (see discussion under *C. mirabilis*). The petiole of the latter species is matte to weakly glossy, sheathed one third to two thirds of its length, and the blades are weakly to moderately bicolorous and usually paler maculate, with the lower surface purple, purple-tinged, or purple-mottled. *Chlorospatha hammeliana* differs in having a semiglossy petiole sheathed one sixth to one fourth of its length and conspicuously

bicolorous, entirely green blades lacking maculations. The similarities of the spadices and floral morphology reflect the sectional relationship between the species. The spadix of *C. mirabilis* is adnate to the spathe one half to three fourths of the length of the pistillate portion, with the pistillate, fertile, and sterile staminate portions of almost equal lengths and the sterile flowers subprismatic. *Chlorospatha hammeliana* differs in having the spadix adnate one fourth to one third of the length of the pistillate portion, with that portion longer, occasionally nearly twice as long as the fertile or sterile staminate portions, and the sterile flowers prominently 4- to 6-lobed or occasionally branched.

The 3-lobed specimen of *Chlorospatha hammeliana* (Croat & Zhu 76881) could possibly be confused with *C. croatiana* subsp. *croatiana*, but all 3-lobed specimens of the latter taxon are moderately to prominently auriculate.

Additional specimens examined. PANAMA. **Coclé:** near Continental Divide, along lumber rd. 5.2 mi. N of El Copé, 1.5 mi. N of lumber camp, 900 m, *Croat 44589* (MO); Alto Calvario, above El Copé, along trail leading W off old lumber trail leading down to Las Ricas, Limón & San Juan, 710–800 m, *Croat 68750* (MO); vic. El Copé, N slope of Cordillera, ca. 1/2 mi. N of Continental Divide, at Alto Calvario, ca. 5.6 mi. N of El Copé, 800 m, *Croat 75071* (CM, MO). **Veraguas:** vic. Escuela Agrícola Alto Piedra near Santa Fé, 0.3 mi. beyond fork in rd. near agricultural school toward Atlantic coast, along trail to top of Cerro Tute, 1050–1150 m, *Croat 48895* (MO); along Santa Fé–Calovébora rd. beyond Escuela Agrícola Alto Piedra, along first major stream, ca. 3 mi. from fork in the rd. at school, 700 m, *Croat 48993* (MO); vic. Santa Fé, along Alto Piedra–Calovébora rd., 0.5 mi. N of Alto Piedra, on slopes of Cerro Tute, Parque Nac. Cerro Tute, 800–1030 m, *Croat & Zhu 76881* (MO).

29. *Chlorospatha hannoniae* Croat, sp. nov. TYPE: Ecuador. Morona-Santiago: Limón–Méndez rd., 940 m, 2°54'49''S, 78°24'04''W, Mar. 1996, *Croat & L. P. Hannon 81477* (holotype, MO-04901596!; isotypes, AAU!, B!, BR!, CAS!, COL!, CUVC!, F!, GB!, GH!, HUA!, INB!, K!, M!, MEXU!, NY!, PMA!, QCA!, QCNE!, RSA!, S!, SEL!, TEX!, U!, UB!, US!, USM!, WU!). Figure 22A–D.

Herba usque ad 50 cm; internodia 1.5–4 × 1.5–2.5 cm. Petiolus 22–27 cm longus, vaginatus per 10–15 cm; lamina foliaris ovato-cordata, interdum late sub-triangularis, 16–20.5 × 10–15.5 cm, lobis posterioribus (5.7–)6–8 × (4.5–)5–7.5 cm, nervis basalibus utroque 2 vel 3, nervis primariis lateralibus utroque (3)4. Inflorescentiae 3 ad 5 in quaque axilla; pedunculus 6–8 cm × 1.2–2.2 mm; spathe 4.5–6 cm longa, tubo 5–7 mm diam., lamina 2.7–4.5 × 7–9 mm diam.; spadix 3.8–5 cm longus.

Terrestrial herb, to 50 cm tall, in small colonies; stem decumbent, erect 10–20 cm, with bulbils

produced randomly and remnants of old leaf bases persisting as a few short fibers along its length; bulbils solitary, green, 5–12 × 3–8 mm, ± ovoid; sap clear; internodes 1.5–4 × 1.5–2.5 cm, matte, dark green, becoming weakly scurfy at nodes with age, drying 1–1.5 cm diam., matte to weakly glossy, medium-dark green; cataphylls ultimately deciduous, 13 per node, erect-spreading, 14–15 cm long, inequilateral, obtuse with acumen at apex (acumen ca. 1 cm long), obtusely 1- to 2-ribbed abaxially, matte, pale green, weakly irregularly darker green-mottled in narrow transverse bands. LEAVES 8 to 14, erect, erect-spreading, spreading to reflexed-spreading; **petioles** 22–27 cm long, glabrous, matte, dark green, weakly darker green-mottled in narrow transverse bands toward base, drying matte to weakly glossy, medium-dark green, sheathed 10–15 cm, ca. 1/2 of total length; sheath free-ending and inequilateral at apex, paler and weakly glossy on inner surface, the sides 5–8 mm wide, widest at base, broadly flaring to 90° midway, appearing winged; free portion ca. 6 mm diam. midway (drying 2–4 mm diam.), U-shaped, entirely obtusely flattened adaxially or only in apical 1/3, the margins bluntly acute toward apex; **blades** held erect, erect-spreading, spreading to reflexed-spreading, ovate-cordate, occasionally broadly subtriangular, 16–20.5 × 10–15.5 cm, 1.1 to 1.6 times longer than wide, weakly acuminate to apiculate at apex, broadest at base, ca. 1.1 times broader at base than across anterior lobe (measured tip to tip across posterior lobes), occasionally narrower at base, occasionally weakly constricted in area of petiole attachment, thinly coriaceous, moderately bicolorous; upper surface broadly quilted and sub-bullate, weakly glossy, dark blackish green, drying matte to weakly glossy, dark green; lower surface reticulate, narrowly minutely colliculate along all venation, weakly glossy, medium green, drying weakly glossy, moderately paler; anterior lobe (14–)16–18 × (10.5–)12.5–14.5 cm, 1.1 to 1.3(1.4) times longer than wide, 2 to 2.3(to 2.7) times longer than posterior lobes, broadest below middle, usually at base, rarely weakly constricted on one side; posterior lobes directed toward the base, occasionally weakly outward, (5.7–)6–8 × (4.5–)5–7.5 cm, 1 to 1.2 times longer than wide, bluntly to narrowly rounded at apex, broadest at base, moderately to prominently inequilateral, the inner side always narrower, weakly to broadly rounded toward base, decurrent onto petiole; outer side 2.2 to 3.1 times wider than inner side midway; all orders of venation matte on lower surface, weakly darker than surface, drying concolorous or weakly to moderately darker than surface; midrib deeply sunken on upper



Figure 22. *Chlorospatha hannoniae* Croat, photos of MO cultivar from the type collection Croat & L. P. Hannon 81477. —A. Potted plant, showing leaf blade adaxial surfaces. —B. Stem with petioles showing the erect-spreading sheaths. —C. Stem with inflorescence at anthesis. —D. Stem with petiole bases and spathe of anthesal inflorescence in side view.

surface, weakly paler than surface toward base, otherwise concolorous, round-raised on lower surface, drying weakly flattened; **basal veins** 2 to 3 pairs, coalesced into a prominent posterior rib; posterior rib round-raised and bluntly acute medially on lower surface, drying raised; primary lateral veins (3)4 pairs, arising at 45°–65°, most acutely toward apex, moderately arcuate, quilted-sunken on upper surface, weakly paler than surface toward base, otherwise concolorous, raised and obtusely angular on lower surface, drying weakly raised to \pm flattened; secondary veins quilted-sunken on upper surface, in part weakly raised and otherwise prominulous on lower surface, drying weakly raised or prominulous; tertiary veins obtusely sunken on upper surface, mostly flat on lower surface, otherwise prominulous, visibly distinct, drying flat, distinct, and visible; reticulate veins weakly obtusely sunken on upper surface, visible, distinct and flat on lower surface, drying visible, distinct, and flat; collective veins 2(3), the innermost arising from apex of posterior rib, loop-connected with all preceding lateral veins, weakly scalloped, 3–8 mm from margin. INFLORESCENCES 3 to 5 per axil, erect, emitting a faint, sweet fragrance at anthesis; sympodium held within a sympodial cataphyll; sympodial cataphyll 4.5–10 \times 1.5–2.5 cm, obtuse with apiculum at apex, obtusely 1- to 2-ribbed abaxially, weakly glossy to semiglossy, pale to medium green; inflorescence cataphyll 2-ribbed abaxially; peduncle 6–8 cm \times 1.2–2.2 mm, cylindroid, thicker than broad, or subterete in apical 2–3 cm, narrowest toward base, weakly glossy, pale to pale-medium green, palest at base, narrowly purple-tinged apically, drying matte, dark brown; **spathe** cucullate, 4.5–6 cm long, oblanceolate, cuspidate at apex, opening narrowly most of length at anthesis, more broadly on blade; spathe tube weakly glossy, medium green, conspicuously purple-tinged in medial 1/3 and at base abaxially, paler and glossy on inner surface, 1.1–2 cm \times 5–7 mm, drying 2.5–4 mm diam., matte to weakly glossy, medium to dark brown on outer surface, weakly glossy and much paler on inner surface; spathe blade matte to weakly glossy, dark maroon to greenish purple, occasionally with the veins medium green on outer surface, glossy, green, with veins and margins deeply purple-tinged on inner surface, 2.7–4.5 cm \times 7–9 mm, 1.4 cm wide (flattened), acutely 1-ribbed abaxially, drying matte to weakly glossy, dark brown on outer surface, rarely greenish, weakly glossy and much paler on inner surface, marcescent, erect after anthesis; **spadix** curving weakly forward, 3.8–5 cm long, sessile, \pm cylindrical, adnate to spathe 2–3 mm at base, 1/4 or less of the length of pistillate portion; pistillate

portion whitish, 0.7–1.2 cm \times 2–4 mm, weakly broadest midway; fertile staminate portion glossy, creamy white, 2.5–3.5 cm \times 3–3.5 mm, weakly ellipsoid, narrowly rounded at apex; sterile staminate portion glossy, white, 0.7–1.2 cm \times 2–3 mm, broadest apically; pistils weakly coherent, 2 to 3 across the axis (viewed from above), 0.6 mm long; ovaries \pm cylindrical or obtusely obconical, white to creamy white, 1–1.3 mm diam., 2-locular, with subaxile placentation and ca. 8 ovules per locule, or rarely 1-locular with a sub-basal placental ring and 10 to 20 ovules on incomplete axis; ovules hemianatropous, 2- to 3-seriate; funicles shorter than ovule; style Type 1 (Fig. 1), white and densely, minutely dark purple-speckled, 1–1.3 mm diam., weakly narrower than to as broad as ovary apex, the margins distinct, not coherent with those of adjacent styles; **stigma** cream-colored, 0.3–0.5 mm diam., sessile, cylindrical, obtusely truncate at apex, depressed medially; synandria ca. 1 \times ca. 2 mm, coherent, occasionally bilaterally symmetrical and weakly elongated in direction of axis, occasionally subrounded, prominently and deeply 2- to 4(5)-lobed (occasionally almost to center), mostly 3- to 4- androus, broadly concave medially, the margins of lobes thickened and sinuate-undulate, weakly interlocking with those of adjacent flowers; pollen creamy white, in tetrahedral tetrads, the exine reticulate; sterile flowers frequently purple-tinged along margins, ca. 0.6 mm long, 1.5–2 \times 0.8–1 mm diam. and \pm elongated in direction of axis, less so in basal whorls, coherent, truncate, irregularly subprismatic, in 3 to 7 whorls. Berries not known.

Phenology. Flowering occurs in *Chlorospatha hannoniae* only during the months of May through September. Sterile collections were made in March and later flowered in cultivation only during those months, over a 5-year period. Inflorescences are fragrant and emerge in quick succession, each reaching anthesis approximately one to three days after anthesis of the preceding inflorescence.

Etymology. *Chlorospatha hannoniae* is named for Mrs. Lynn P. Hannon (1948–2006), of Odessa, Florida, an associate of the University of South Florida, whose many field trips to Ecuador and excellent living collections made this revision substantially more complete (please see dedication footnote at beginning of manuscript).

Discussion. *Chlorospatha hannoniae* is known only from the type collection made along the road between Limón and Méndez, in premontane moist forest on the eastern slopes of the Andes, at 940 m

elevation. The species would be expected to occur elsewhere within the province and possibly to the south in Zamora-Chinchipe Province and eastward into Peru.

Chlorospatha hannoniae, a member of *Chlorospatha* sect. *Orientalis*, is found in small colonies and is distinguished by its sub-bullate, weakly glossy, dark blackish green, broadly ovate-cordate leaf blades with the posterior lobes more or less rounded at the apex, approximately half as long as the anterior lobe and frequently overlapping on the inner sides. Although it is a robust plant with stems to 2.5 cm in diameter, it is less than 50 cm tall and has eight to 14 leaves held erect, erect-spreading, spreading, and reflexed-spreading. The petioles are short (22–27 cm long), relative to blade length, almost as long as the blades and sheathed approximately half of the total length, with the sides of the sheath broadly flaring, thus appearing winged, a condition observed in only one other species. *Chlorospatha hannoniae* is also distinguished by producing cataphylls only during the flowering cycle. The inflorescence is small, no more than 6 cm long, with the spathe tube maroon-tinged green and the blade dark maroon. The species is also distinguished by its white ovaries and styles, with the latter densely, minutely dark purple-speckled. The glossy, white, staminate portion of the spadix is also distinctive, with the sterile portion almost as long as the pistillate portion, unusual for species from the eastern slopes.

Chlorospatha hannoniae is probably most closely allied and would be most easily confused with *C. boosii* (see discussion under *C. boosii*).

Chlorospatha hannoniae could possibly be confused with *C. longipoda*, which is widespread on the eastern slopes of the Andes in Ecuador, at 470–1700 m elevation, and is probably sympatric with *C. hannoniae* in Morona-Santiago Province (see discussion under *C. longipoda*). *Chlorospatha hannoniae* is a more robust plant when mature, with stems to 2.5 cm diameter versus 1.3 cm diameter in mature specimens of *C. longipoda* in which the remnants of old cataphylls and petiole bases are retained more or less intact along the length of the stem, differing from *C. hannoniae* in which only the petiole bases are retained as a few short fibers.

30. *Chlorospatha hastata* Croat & L. P. Hannon, sp. nov. TYPE: Ecuador. Esmeraldas: Lita–San Lorenzo rd., 3.4 km E of El Durango, 17.3 km W of Alto Tambo, 375 m, 1°12'31"N, 78°37'02"W, 8 July 1998, Croat, L. P. Hannon, D. Mansell & J. Whitehill 82531 (holotype, MO-04889546!; isotypes, B!, CAS!, F!, K!, NY!, US!). Figures 23A–D, 24A.

Herba usque ad 1 m; internodia 0.5–1.5 × 1–2 cm; cataphylla 16–37 cm longa. Petiolus 35–69 cm longus, vaginatus per 15–33 cm; lamina foliaris hastata, 19–32 × 20–33 cm, lobis posterioribus 10.5–20 × (3.2–)4–7 cm, nervis basalibus utroque 6 ad 9, nervis primariis lateralibus utroque 7 vel 8. Inflorescentiae 1 vel 2 in quaque axilla; pedunculus 15–25 cm × 2–4 mm; spatha 9–13.5 cm longa, tubo 0.5–1.2 cm diam., lamina 4–6.5 cm × 8–9 mm diam.; spadix 5.3–9.2 cm longus.

Terrestrial herb, to 1 m tall; stem decumbent, erect to 20 cm, remnants of old leaf bases and cataphylls persisting as a few short fibers along its length; sap milky; internodes 0.5–1.5 × 1–2 cm, semiglossy, medium to dark green, drying weakly glossy, medium gray-tinged brown; cataphylls 16–37 cm long, obtuse with acumen at apex (acumen to 3 mm long), obtusely 1-ribbed abaxially in apical 1/2, pale green, weakly darker purple-mottled in narrow transverse bands, drying weakly glossy to semiglossy, medium-dark reddish brown. LEAVES 2 to 3, erect-spreading; **petioles** 35–69 cm long, glabrous, matte, pale to medium green, moderately to densely purple-mottled in narrow transverse bands, most densely so toward base, rarely greenish adaxially and otherwise entirely purplish and darker purple-mottled, drying matte to weakly glossy, medium to dark brown, sheathed 15–33 cm, 1/3 to 1/2 of total length; sheath free-ending at apex; free portion 3–6 mm diam. midway, terete, narrowly sulcate; **blades** hastate, 19–32 × 20–33 cm, 1 to 1.2(to 1.4) times longer than wide, usually as wide as long to occasionally 1.2 times wider than long, gradually acuminate to narrowly acuminate at apex, broadest at base, 3 to 4 times wider at base than across anterior lobe (measured tip to tip across posterior lobes), thin, markedly bicolorous; upper surface velvety to matte-subvelvety, dark green, drying dark green to olive-green, rarely brown; lower surface semiglossy, rarely weakly glossy, pale green and markedly discolorous, narrowly to ± broadly dark purple along midrib and major veins, drying semiglossy to glossy, green to brownish, weakly to moderately paler and usually markedly discolorous; anterior lobe 15.5–22 × 5–11 cm, 1.9 to 2.8(to 3.4) times longer than wide, 1.1 to 1.5 times longer than posterior lobes, broadest at or below middle, moderately to markedly constricted at base, ± symmetrical; posterior lobes directed prominently outward, 10.5–20 × (3.2–)4–7 cm, 2.4 to 3.6(to 4) times longer than wide, acute to bluntly acute at apex or weakly acuminate with the tip bluntly acute, broadest midway, usually markedly constricted at base, ± symmetrical, the inner side weakly to broadly rounded toward base, briefly attenuate onto posterior rib; outer side ± straight toward base; midrib and major venation moderately to deeply



Figure 23. *Chlorospatha hastata* Croat & L. P. Hannon, photos of the type collection *Croat et al.* 82531 (MO). —A. Fertile habit. —B. Leaf blade abaxial surfaces. —C. Petiole with inflorescence at anthesis. —D. Anthesal inflorescence with spathe tube open to expose entire spadix.

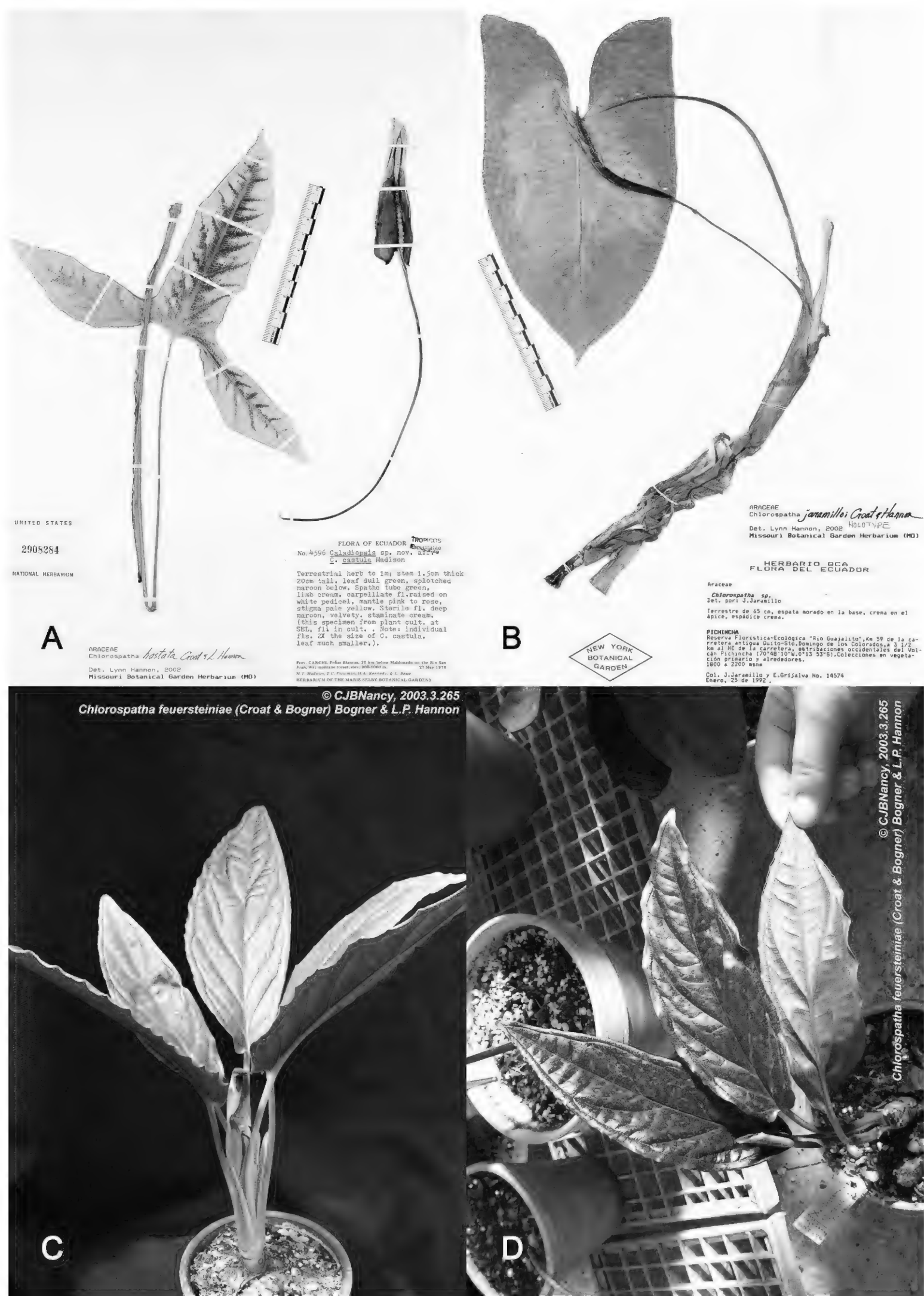


Figure 24. —A. *Chlorospatha hastata* Croat & L. P. Hannon, paratype specimen *Madison et al.* 4596 (MO). —B. *Chlorospatha jaramilloi* Croat & L. P. Hannon, *Jaramillo & Grijalva* 14574 (NY holotype specimen). C, D. *Chlorospatha feuersteiniae* (Croat & Bogner) Bogner & L. P. Hannon. —C. Habit of potted plant. —D. Habit showing purple underside of leaf. Photos used by permission of Nancy Botanical Garden.

sunken on upper surface, weakly granular-puberulent on lower surface, \pm dark purple, drying weakly raised and \pm flattened, weakly to moderately darker than surface, usually purplish; midrib round-raised on lower surface, occasionally minutely ribbed; **basal veins** 6 to 9 pairs, coalesced into a prominent posterior rib; posterior rib naked 1–2 cm per side; primary lateral veins 7 to 8 pairs, arising at (30° – 40° – 60° – 70°), weakly to moderately arcuate, occasionally \pm straight, convex on lower surface; secondary veins raised, frequently in part dark purple on lower surface, drying weakly raised or prominulous, rarely moderately raised, darker than surface; tertiary veins raised or prominulous on lower surface, drying entirely prominulous or in part prominulous and otherwise flat, concolorous to weakly darker than surface; reticulate veins obscure; collective veins 3(4), the innermost arising from lowermost lateral vein on inner side of posterior lobe, loop-connected with all preceding lateral veins, parallel to margin or weakly scalloped, 3–4(–10) mm from margin. INFLORESCENCES erect, 1 to 2 per axil, emitting a sweet or musty-fruity fragrance at anthesis; peduncle held within the sheath, terete to elliptical or terete midway and obtusely D-shaped or U-shaped toward apex, 15–25 cm \times 2–4 mm, narrowest toward base, pale green, weakly irregularly darker purplish mottled in narrow transverse bands, drying matte to weakly glossy, medium to dark brown, occasionally dark green; **spathe** \pm erect, 9–13.5 cm long, lanceolate, weakly cuspidate at apex, the margins in-rolled toward apex, opening broadly at anthesis, nearly to base, the margins directed forward; spathe tube weakly glossy to semiglossy, medium to medium-dark green on outer surface, matte to weakly glossy and moderately paler on inner surface, occasionally with the longitudinal veins weakly darker on both surfaces, 5–7 \times 0.5–1.2 cm, drying matte to weakly glossy or semiglossy, dark brown to dark green on outer surface, matte to weakly glossy, concolorous to weakly paler on inner surface; spathe blade weakly glossy to semiglossy, greenish cream to yellow-green cream on outer surface, matte on inner surface (rarely semiglossy), concolorous, occasionally with longitudinal veins weakly darker than surface, 4–6.5 cm \times 8–9 mm, 2–3.2 cm wide (flattened), drying matte to weakly glossy, brownish cream to yellow-green cream, rarely tinged reddish brown, marcescent, erect after anthesis; **spadix** erect, stipitate 1–1.8 cm, 5.3–9.2 cm long, adnate to spathe 0.9–1.7 cm at base, only along stipe, the stipe frequently emerging from a sheath in the spathe, with sheath margins to 1 mm wide; pistillate portion pink or pale purplish, 2.5–4.7 cm \times 4–6 mm, broadest

midway or toward apex, drying purplish; fertile staminate portion cream to yellowish cream or yellow-green cream, (1.4–)2.4–3.3 cm \times 2.5–6 mm, narrowly rounded to bluntly acute at apex, terete to weakly cylindroid (thicker than broad), broadest at or below middle, \pm cylindrical to tapering, drying pale to dark tan; sterile staminate portion \pm purple to dark maroon, 1–2.7 cm \times 2.5–4 mm, usually broadest at base; pistils \pm laxly arranged, ca. 3 across the axis (viewed from above), 1.2–2 mm long; ovaries white, cream, or greenish cream (rarely tan), \pm subglobose, 1.7–2 mm diam., 2- to 3(4)-locular, with subaxile placentation; ovules 4 to 8 per locule, small, anatropous, biseriate; funicles longer than ovules; style Type 4 (Fig. 1), rarely tan (post-anthesis), 2–2.5 mm diam., 0.15 mm thick, obscurely attenuate, markedly broader than ovary apex, with red chromoplasts present, the margins frequently \pm coherent with those of adjacent styles; **stigma** pale orangish yellow to orangish white, rarely tan-white, 0.5–1 mm diam., appearing sessile, \pm cylindrical to obconical, depressed medially, obscurely elevated on style; synandria 1–1.5 \times 1.2–2.3 mm, coherent, truncate, (2)3- to 4(5)-lobed, mostly 3- to 4-androus, occasionally with some flowers at apex 1- to 2-lobed and lacking microsporangia; thecae oblong; pores apical; sterile flowers entirely purple to maroon or in part cream medially and purple to maroon on sides, rarely with some flowers entirely cream (on same spadix), ca. 1 mm long, 2–3 \times 1 mm diam. and \pm elongated in direction of axis, fungiform, broadly and deeply concave medially, frequently almost to base, the margins markedly sinuate-undulate, \pm laxly arranged, in 4 to 8 whorls. INFRUCTESCENCE (immature) 8 cm \times 11 mm, drying dark purplish brown; berries (immature) ca. 3 mm diam., drying brownish white.

Phenology. Flowering is only known to occur in *Chlorospatha hastata* during the months of May, July, August, and December. Inflorescences emerge in slow progression, with several days between anthesis of one inflorescence and emergence of the next inflorescence at the apex of the petiole sheath. In cultivation, flowering is not continuous but periodic.

Etymology. The epithet is taken from the Latin “hastatus,” meaning “hastate,” with the posterior lobes of *Chlorospatha hastata* directed outward.

Discussion. *Chlorospatha hastata* is known only from premontane wet forest on the western slopes of the Andes in Carchi and Esmeraldas provinces in northern Ecuador, at 375–1800 m elevation. The species is likely to occur also in southern Colombia,

there being no significant differences in the habitat or conditions there.

Chlorospatha hastata is a member of *Chlorospatha* sect. *Occidentales* and is distinguished by its hastate, velvety, dark green leaf blades, usually as wide as long, with the lobes prominently constricted at the base, the lower surface conspicuously paler and usually sharply and narrowly or broadly discolored dark purple along the major veins. The thin, pink to purplish, broadly spreading style, much broader than the ovary apex and obscurely attenuated, the long sterile staminate portion of the spadix, which comprises one fourth to one third of total length, and unusual concave-fungiform sterile flowers are also noteworthy. The attenuated portion of the style is markedly short and obscured by the mantle; therefore, the stigma only appears to be sessile. The sterile flowers are laxly arranged; deeply concave medially, either sessile or weakly stipitate and usually entirely dark purple, occasionally with the concave portion white or cream-colored. The long sterile staminate portion of the spadix, with these unusual flowers, is a condition found in only two other species, either of which might be confused with *C. hastata*: *C. atropurpurea* and *C. castula*. All three species have leaf blades that are velvety, dark green on the upper surface and either purple-tinged, dark purple-mottled, or entirely purple on the lower surface.

Chlorospatha atropurpurea and *C. hastata* share the same striking coloration on the lower surface of the blade, whereas in *C. castula*, the surface is only purple-tinged medially or entirely green with the major veins purplish. The spathe is cucullate in *C. atropurpurea* and *C. castula*, but erect in *C. hastata* (see discussions under both species).

The label notes for *D. Rubio et al.* 1733 report that in Carchi Province, the fruits are used for snakebites and the local name for the species is “papa de la culebra.”

Paratypes. ECUADOR. **Carchi:** Peñas Blancas, 20 km below Maldonado, 900–1000 m, May 1978, *Madison et al.* 4596 (MO, QCA, SEL, US-2908284); 45 km below Maldonado, Nov. 1979, *Madison & Besse* 7080 (SEL); Tulcán Cantón, Res. Indígena Awá, Gualpi Alto comm., Chical parish, 1800 m, 1°02'N, 78°14'W, 15–28 June 1991, *D. Rubio, C. Quelal & P. Nastacuaz* 1733 (MO, QCNE); Res. Vida Awá, 2004, *G. Toasa* 9580 (QCNE). **Esmeraldas:** vic. Alto Tambo, along Lita–San Lorenzo rd., 17.1 km W of Río Lita near Lita, 822 m, 0°54'06"N, 78°32'27"W, 20 July 2000, *Croat, L. P. Hannon, D. Hannon, G. Walhert & K. Tuniak* 84232 (MO).

31. *Chlorospatha hastifolia* Bogner & L. P. Hannon, Willdenowia 37: 334–336. 2007. TYPE: Colombia. Comisaria del Amazonas, confluencia de

los ríos Amazonas y Loretoyacu. 12 Apr. 1975, *I. Cabrera* 3353 (holotype, COL-184576!). Figure 46D.

Plant glabrous, with short stem and 3 leaves; stem ca. 2.5 cm long and ca. 0.8 cm in diam., covered with branched roots, those of first order ca. 0.5 mm in diam. LEAVES; **petiole** 25–27 cm long and ca. 0.3 cm in diam., purple; sheath 11.5–12.5 cm long; **blade** hastate, coriaceous, 25–27 × 7–7.5 in the middle; anterior lobe ca. 20 × 7–7.5 cm, apex of anterior lobe cuspidate; basal lobes 7–7.5 × 2 cm, apex ± obtuse; venation reticulate; 4 to 5 primary lateral veins on each side of a strong midrib, one of the primary lateral veins running into each basal lobe, second order veins forming an interprimary collecting vein, third and fourth order veins forming an irregular network (well visible underneath); inner collective vein 4–5 mm from the margin, second outer collecting vein thinner and 0.9–1.5 mm from the margin, also a very thin third collective vein running along the margin. INFLORESCENCE; peduncle ca. 7 cm long and placed within the leaf sheath; **spathe** incomplete, but clearly constricted (purple testae collector's notes); lower part ellipsoid, ca. 1.5 cm long and ca. 0.8 cm in diam. at the constriction ca. 0.3 cm in diam., upper part of spathe lacking; **spadix** ca. 6 cm long (cream-colored testae collector's notes), fertile to apex and narrowing toward apex; female part ca. 1.2 cm long and 0.4 cm in diam.; male part 4–4.2 cm long and 0.5 cm in diam.; sterile part between female and male flowers ca. 1.5 cm long, at most of its length 1.8–2 mm in diam., at base 3 mm in diam. FLOWERS unisexual, naked; female flowers somewhat laxly arranged; ovary 0.9–1(–1.1) mm in diam.; **stigma** button-like, yellow, ca. 0.4 mm in diam.; style broader, 0.9–1 mm in diam., somewhat lobed (usually 4-lobed), thin, dark-colored, not coherent; synandria somewhat laxly arranged; synandrium truncate, ca. 1 mm tall, from above irregularly rectangular to ± elliptic, 1.2–1.5 × 0.8–1 mm, with incisions of the thecae (as seen from above), thecae lateral, ca. 1 mm long (thecae still closed in the specimen); pollen grains in tetrads, 55–60 µm in diam., exine smooth (psilate); synandrodies between female and male flowers very long and narrow, truncate, ± linear and narrowed at both ends, very slightly sunken in the center, from above 2.5–3 × 0.3–0.4 mm, the lowermost up to 1 mm wide and narrowly lanceolate in shape. Berries unknown.

Phenology. The type specimen flowered in April.

Discussion. *Chlorospatha hastifolia* is only known from the type locality. It was collected at the junction

of the rivers Amazonas and Loretoyacu, where it grows on red heavy sandy soil (laterite) in a half-shaded place.

Chlorospatha hastifolia is a member of *Chlorospatha* sect. *Occidentales*.

32. *Chlorospatha huilensis* Croat & L. P. Hannon, sp. nov. TYPE: Colombia. Huila: Finca Merenberg, 100 km E of Popoyán, 2300 m, 5–6 Dec. 1980, *Croat 51944* (holotype, MO-2886244!; isotype, COL-308247!). Figure 25A–D.

Herba 0.3–1 m; internodia (1–)1.5–3.5 × 1–2 cm; cataphylla 11.5–18 cm longa. Petiolus 21.5–43.5 cm longus, vaginatus per 12–21 cm; lamina foliaris sagittata vel debiliter subhastata, (11.4–)16–23 × (5.5–)8–12.7 cm, lobis posterioribus (4.5–)5.5–9.4 × (1.8–)2.8–4.5 cm, nervis basalibus utroque (2)3 vel 4, nervis primariis utroque 3 ad 5. Inflorescentiae 2 ad 5 in quaque axilla; pedunculus 8–14.5 cm × 1–2 mm; spatha 6–10.5 cm longa, tubo 3–4.5 cm × 3.5–6 mm; spadix 5.3–8.5 cm longus.

Terrestrial herb, 0.3–1 m tall; stem decumbent, remnants of old cataphylls persisting ± intact at upper nodes; internodes (1–)1.5–3.5 × 1–2 cm, drying weakly glossy, pale grayish brown to medium brown (all measurements made from dried material); cataphylls 11.5–18 cm long, abruptly acuminate at apex, drying weakly glossy to semiglossy, medium orangish brown, occasionally paler. LEAVES 3 to 4, erect-spreading; **petioles** 21.5–43.5 cm long, glabrous, weakly glossy, medium-dark pink-tinged green, finely and irregularly darker transversely lineate in basal 1/2, drying weakly glossy, dark reddish or orangish brown to almost black (apically), paler near base, sheathed 12–21 cm, ca. 1/2 of total length; sheath free-ending at apex; free portion 1–3 mm diam. midway, terete or subterete; **blades** sagittate to weakly subhastate, (11.4–)16–23 × (5.5–)8–12.7 cm, 1.7 to 2 times longer than wide, acuminate at apex, rarely acute or abruptly acuminate, broadest at base, 1.4 to 1.6 times wider at base than across anterior lobe (measured tip to tip across posterior lobes), weakly or not at all constricted in area of petiole attachment, thin, moderately bicolorous; upper surface possibly bullate, semiglossy, dark green, drying matte to weakly glossy, medium to medium-dark yellowish brown (rarely green); lower surface semiglossy, drying matte to weakly glossy (glossier than upper surface), weakly paler or concolorous; anterior lobe (8–)11.5–17.5 × (4–)6.5–8.8 cm wide, 1.7 to 1.9(to 2.1) times longer than wide, 2.2 to 2.4(to 2.6) times longer than posterior lobes, broadest at or near base, symmetrical to weakly inequilateral; posterior lobes directed toward the base or occasionally weakly outward, (4.5–)5.5–9.4 ×

(1.8–)2.8–4.5 cm, (2.1 to)2.3 to 2.9 times longer than wide, bluntly acute at apex, rarely narrowly rounded, broadest at base, moderately inequilateral, the inner side narrower, weakly rounded toward base, briefly to moderately attenuate and weakly confluent with opposite lobe at base, obscuring petiole apex; outer side 1.8 to 2 times wider than inner side midway, ± straight toward base; all venation (except reticulate) markedly impressed on upper surface, prominently raised on lower surface, weakly granular-puberulent and matte; midrib and major veins round-raised on lower surface, drying round-raised, concolorous or weakly to moderately darker than surface; **basal veins** (2)3 to 4 pairs, coalesced into a prominent posterior rib; primary lateral veins 3 to 5, arising at 25°–60°(–70°), most acutely toward apex, straight to moderately arcuate; secondary veins drying raised on lower surface, concolorous to weakly or moderately darker than surface; tertiary veins drying entirely raised or in part raised and otherwise prominulous on lower surface, weakly darker than surface; reticulate veins drying ± prominulous on lower surface, concolorous to weakly darker than surface; collective veins 3, the innermost arising from lowermost lateral vein on inner side of posterior lobe, rarely from apex of posterior rib, ± parallel to and 3.5–9 mm from margin. INFLORESCENCES erect, 2 to 5 per axil; peduncle held within the sheath, 8–14.5 cm × 1–2 mm, narrowest at base, weakly glossy, pale green, irregularly weakly darker transversely lineate in basal 2/3, drying matte to weakly glossy, dark blackish brown, occasionally paler toward base; **spathe** 6–10.5 cm long, weakly cucullate, cuspidate at apex; spathe tube pale to medium green on outer surface, 3–4.5 cm × 3.5–6 mm, drying weakly glossy, dark blackish brown; spathe blade white or yellow, 3.2–6 cm × ca. 7 mm, drying matte to weakly glossy, pale tan or orangish tan to occasionally medium-dark brown on outer surface, paler on inner surface, opening broadly at anthesis, marcescent, erect after anthesis; **spadix** erect, 5.3–8.5 cm long, sessile, adnate to spathe 3–4.2 cm at base, entire length of pistillate portion; pistillate portion greenish, 3–4.2 cm × 2.5–3 mm, narrowest at base, drying medium brownish; fertile staminate portion white or dark yellow, 2.5–4.5 cm × 3–5 mm, acute to bluntly acute at apex, ± ellipsoid, broadest at or below middle, drying pale grayish tan to yellowish; sterile staminate portion 6–9 × 1.5–2 mm, broadest at apex, drying yellowish tan; pistils weakly coherent, 2 to 4 across the axis (viewed from above), 1.5–1.9 mm long; ovaries subglobose, 0.6–0.8 × 1.5–2.5(–3) mm, drying pale tan with darker veins; style Type 5 (Fig. 1), ca. 2 × ca. 1.6–2.2 mm (attenuate portion to ca. 0.8 mm long), greenish,



Figure 25. *Chlorospatha huilensis* Croat & L. P. Hannon. A–C. Photos and images for the type collection, *Croat 51944* (MO). —A. Fertile habit. —B. Isotype specimen (COL-308247). —C. Inflorescence post-anthesis. —D. Paratype specimen of *C. huilensis*, *Croat 51832* (COL-306928).

comprising ca. 1/2 of the length of pistil, much broader than ovary apex, the margins \pm weakly coherent with those of adjacent styles; **stigma** ca. 0.3 mm diam., elevated on and broader than narrowed portion of style; synandria 1–1.2 \times 1–1.2 mm, coherent, truncate, deeply (2)3- to 4-lobed, mostly 3- to 4-androus; sterile flowers ca. 1 mm long, 1–2 \times 1 mm diam. and \pm elongated in direction of axis, coherent, truncate, irregularly subprismatic, in 3 to 4 whorls. Berries not known.

Phenology. Flowering is only known to occur in *Chlorospatha huilensis* during the months of August and December.

Etymology. The epithet is taken from the name for Huila Department of Colombia, in which the type locality of *Chlorospatha huilensis* is located.

Discussion. *Chlorospatha huilensis* is known from the southern end of the Magdalena River drainage between the Cordilleras Central and Oriental in southern Colombia, at 2000–2420 m elevation in Huila Department, and rarely from the Amazon drainage in Putumayo Department. The species appears to be endemic to this area of premontane rainforest and lower montane rainforest, though it possibly occurs also in the broad areas of lower montane wet forest that border the rainforest. The species would be expected to occur in that portion of Nariño Department that lies between Huila and Putumayo departments on the eastern slopes and possibly southward into northern Ecuador. It is one of only two species in *Chlorospatha* sect. *Occidentales* that occurs exclusively or occasionally on the eastern slopes of the Andes.

Chlorospatha huilensis is distinguished by its long internodes (1.5–3.5 cm) and usually sagittate, semiglossy, dark green leaf blades with all venation but the reticulate markedly impressed on the upper surface and prominently raised and matte on the lower surface. The posterior lobes are weakly confluent at the base, obscuring the petiole apex. The species is also distinguished by its short peduncles (less than 15 cm long) and greenish styles.

Chlorospatha huilensis could be confused with *C. antioquiensis* from the Magdalena River drainage in Antioquia Department, Colombia, at 1800–3000 m elevation (see discussion under *C. antioquiensis*).

Chlorospatha bullata also might be confused with *C. huilensis*. *Chlorospatha bullata* occurs only on the western slopes of the Cordillera Occidental in Valle Department. In the latter species, the petiole is purple-tinged, occasionally the lower blade surface as

well, differing from *C. huilensis* in which both are entirely green (see discussion under *C. bullata*).

Chlorospatha huilensis might be confused with *C. congensis* from Cauca Department on the western slopes of the Cordillera Occidental in Colombia, which differs in having shorter internodes, the petiole sheath decurrent at the apex and leaf blades that dry subcoriaceous, with the upper surface velvety-matte (see discussion under *C. congensis*).

Chlorospatha huilensis is also similar to *C. sucumbensis*, a species known only from the eastern slopes of the Andes in Sucumbíos Province in northernmost Ecuador, along the El Carmelo–La Bonita road that parallels the border with Colombia, at 2200–2350 m elevation. In *C. huilensis*, the petiole is sheathed one half of its length; the internodes dry pale grayish brown to medium brown, and the blades dry yellowish brown and not reticulate on the lower surface, with all venation weakly darker than the surface (see discussion under *C. sucumbensis*).

Idrobo et al. 2869 was previously filed as *Chlorospatha lehmannii* by Madison (1981), but was found to accord with *C. huilensis* in all respects. This collection differs from the type of *C. huilensis* in having dark yellow (not white) synandria. *Chlorospatha lehmannii* differs from *C. huilensis* in having coriaceous leaf blades that are velvety on the upper surface, with the posterior lobes narrower, longer (relative to the length of the anterior lobe), and directed outward. The posterior rib is naked 5–7 mm per side, with the inner margin decurrent onto the posterior rib. The blades of *C. huilensis* are thin and semiglossy on the upper surface, with the posterior lobes directed toward the base and weakly confluent at the base, obscuring the petiole apex. The major venation dries flattened on the lower surface in *C. lehmannii*, but for the most part is raised in *C. huilensis*. The peduncle, spathe, and spadix are longer in *C. lehmannii*, with the pistils laxly arranged and Type 7 styles (Fig. 1). *Chlorospatha huilensis* has weakly coherent pistils and Type 5 styles (Fig. 1). The sterile flowers of *C. lehmannii* are fungiform or branched, whereas those of *C. huilensis* are subprismatic.

Paratypes. COLOMBIA. **Huila:** Finca Merenberg, 100 km E of Popayán, 2300 m, 5–6 Dec. 1980, *Croat 51911* (MO); Macizo Colombiano, Hoya del Magdalena, Km. 17 on San Agustín–Santa Rosa rd., “La Candela,” 2420 m, 27 Aug. 1958, *J. Idrobo, Pinto & Bischler 2869* (P). **Putumayo:** along Pasto–Macoa rd., vic. Km. 95, near Restaurante Buenos Aires; ca. 2000 m, 3 Dec. 1980, *Croat 51832* (COL-306928, MO).

33. *Chlorospatha ilensis* Madison, Selbyana 5(3–4): 355. 1981. TYPE: Ecuador. Pichincha: path following ridgeline at La Centinela at crest of

Montañas de Ila, at Km. 12 on Patricia Pilar–24 Mayo rd., 600 m, 6 Feb. 1979, *C. Dodson, A. Gentry & J. Duke* 7547 (holotype, SEL!; isotypes, MO!, QCNE!, RPSC not seen). Figure 26A–D.

Terrestrial herb, rarely hemiepiphytic, over 1 m tall; stem erect, 5–24 cm long, cylindrical, with remnants of old cataphylls persisting intact at upper few nodes, otherwise as pale fibers, with bulbils produced in basal 1/3; bulbils solitary, ovoid, ca. 5×5 mm on exposed stem, elongated below soil surface and $10 \text{ cm} \times 5 \text{ mm}$; sap clear; internodes $1\text{--}1.5 \times 1\text{--}4$ cm, weakly scurfy, dull tan, drying matte, medium-dark to dark brown; cataphylls 10–30 cm long, obtuse with acumen at apex (acumen 1–5 mm long), weakly glossy, pale to medium green, entirely irregularly finely purple-mottled in narrow transverse bands, most densely so toward base, occasionally entirely purple-tinged on outer surface, semiglossy and much paler on inner surface, drying weakly glossy to semiglossy, medium-dark to dark reddish or orangish brown. LEAVES 3 to 5, erect-spreading; **petioles** 43–100 cm long, moderately firm, rarely fleshy, glabrous, matte to weakly glossy, dark purple for most of length, or green apically and darker purple-mottled toward base, or entirely pale yellow-green to medium-dark green or weakly olive-green and pale to moderately dark maroon- or purplish-mottled, most densely so toward base, rarely entirely medium green with sheath margins dark maroon when in flower, drying weakly glossy to semiglossy (rarely matte), medium to dark brown, sheathed 22.5–60 cm, 1/2 to 2/3 of total length (ca. 1/4 when sterile); sheath decurrent at apex, rarely free-ending, rarely with margins weakly undulate; free portion 5–10 mm diam. midway, terete or subterete, occasionally obtusely 1-ribbed medially; **blades** held horizontally, hastate or deeply 3-lobed, occasionally subhastate, $24\text{--}40.5 \times 27\text{--}56$ cm, usually wider than long, gradually or narrowly acuminate at apex, rarely abruptly acuminate, broadest at base, 2.6 to 3.6(to 4.2) times wider at base than across anterior lobe (measured tip to tip across posterior lobes), thin, moderately bicolorous; upper surface quilted, semiglossy to glossy, medium green, drying weakly glossy to semiglossy, dark greenish brown to olive-brown or olive-green, rarely grayish green; lower surface glossy, drying semiglossy to glossy, weakly to moderately paler; anterior (or medial) lobe $16.5\text{--}32 \times 7\text{--}19$ cm, 1.7 to 2.6 times longer than wide, 1.1 to 1.4 times longer than posterior (or lateral) lobes, usually broadest at or below middle, rarely above middle, moderately to markedly constricted at base, weakly inequilateral; posterior lobes directed outward, frequently toward

the apex on drying, $13.5\text{--}28 \times (4\text{--})5.5\text{--}13.5$ cm, 1.8 to 2.9(to 3.7) times longer than wide, acuminate at apex, rarely acute or narrowly rounded, broadest at or below middle, usually markedly constricted at base (weakly to moderately constricted in young plants), weakly to moderately inequilateral, occasionally markedly so, the outer side narrower, straight to weakly concave toward the base; inner side (1)1.1 to 3(to 4.3) times wider than outer side midway, weakly to broadly rounded toward base and briefly to gradually attenuate onto posterior rib, occasionally decurrent onto petiole; **lateral lobes** (when present) as per posterior lobes but directed toward the apex, narrowly confluent with medial lobe, the confluent portion 1–2 cm wide; midrib and major venation sunken on upper surface, concolorous to weakly paler on lower surface, drying \pm flattened, prominently darker than surface, occasionally moderately darker; midrib round-raised on lower surface; **basal veins** (or primary lateral veins on lateral lobes) (5)6 to 9 pairs, coalesced into a prominent posterior rib; posterior rib naked 3–9 mm per side, occasionally not at all; primary lateral veins (5)6 to 9(10) pairs, arising at $(35^\circ\text{--})45^\circ\text{--}90^\circ$, most acutely toward apex, straight to weakly arcuate, or in part moderately arcuate or irregularly ascending, convex on lower surface; secondary veins obtusely sunken on upper surface, raised on lower surface, drying weakly to moderately raised, usually darker than surface; tertiary veins distinct, visible on lower surface, drying distinct, in part weakly prominulous, otherwise flat, darker than surface; reticulate veins obscure; collective veins 3, arising from one of the lowermost lateral veins on inner side of posterior (or lateral) lobe, loop-connected with all preceding lateral veins, \pm parallel to margin, occasionally moderately scalloped, 2–7(–10) mm from margin. INFLORESCENCES erect to erect-spreading, 5 to 6 per axil, emitting a sweet mintlike to spicy fragrance at anthesis; peduncle held within the sheath, $21\text{--}57 \text{ cm} \times 1\text{--}4 \text{ mm}$, cylindroid, thicker than broad, or terete and obtusely flattened adaxially toward apex, narrowing toward base, weakly glossy to semiglossy, pale green to yellow-green or medium green, occasionally finely, irregularly, weakly darker-mottled, most prominently toward base, drying weakly glossy to semiglossy, medium-dark to dark brown, rarely greenish brown; **spathe** cucullate, 7.5–12 cm long, \pm acute at apex, occasionally weakly cuspidate, opening broadly most of its length at anthesis, the margins directed forward or occasionally somewhat outward; spathe tube matte to semiglossy, pale to medium green or yellow-green on outer surface, glaucous medially toward apex, frequently narrowly conspicuously paler at margins, glossy on



Figure 26. *Chlorospatha ilensis* Madison. A–C. Cultivar at Selby 79-1718 from *Dodson et al.* 9135 (MO). —A. Leaf with anthesis inflorescence evident on petiole. —B. Leaf blade adaxial surface. —C. Inflorescence at anthesis, with the spathe tube cut open. —D. Fertile cultivar of *Croat* 57003 (MO).

inner surface, $3.5\text{--}6 \times 0.6\text{--}1.3$ cm, drying matte to weakly glossy, medium to dark brown or greenish brown on both surfaces; spathe blade matte to semiglossy, pale green to yellow-green, occasionally cream near apex or entirely creamy white to greenish cream and narrowly pale green medially on outer surface, matte to weakly glossy on inner surface, $4\text{--}7 \times 0.8\text{--}1.2$ cm, to 2.5 cm wide (flattened), obtusely 1-ribbed abaxially, drying matte to weakly glossy, medium to dark brown or greenish brown on both surfaces, usually weakly paler than tube, marcescent, erect after anthesis; **spadix** curved weakly forward, 5.5–10 cm long, sessile to weakly stipitate (to 3 mm), adnate to spathe 0.8–2.5 cm at base, ca. 1/3 to 1/2 of the length of pistillate portion; pistillate portion pale green to dull or bright yellow-green, $(1.9\text{--})2.6\text{--}5$ cm \times 3–5.5 mm, weakly broadest midway, drying medium to dark brown or medium greenish; fertile staminate portion cream-colored, pale green to yellow-green or greenish white, $2.5\text{--}4.7$ cm \times 4.5–6 mm, narrowly rounded at apex, \pm cylindrical or weakly tapering, occasionally weakly thicker than broad, drying tan to dark brown; sterile staminate portion cream-colored, $5\text{--}10 \times$ ca. 4 mm, \pm cylindrical; pistils weakly coherent, ca. 4 across the axis (viewed from above), 1–1.3 mm long; ovaries pale green or greenish white, \pm cylindrical, obtusely truncate at apex, 1.3–2 mm diam., drying pale brownish white with darker veins, 2-locular, with axile placentation, 10 to 12 ovules per locule, the ovules small, hemianatropous, biseriate; funicles shorter than ovules; style Type 3 (Fig. 1), 1.2–1.5 mm diam., weakly broader than ovary apex, the margins weakly sinuate and not coherent with those of adjacent styles; **stigma** pale yellow-green to white, 0.5–0.8 mm diam., sessile, obtusely truncate; synandria $1\text{--}1.4 \times 1.5\text{--}2.5$ mm, coherent, truncate, 2- to 5-lobed, (2)3- to 5-androus (mostly 4); sterile flowers 0.8–1.2 mm long, $1.5 \times 2.2\text{--}3$ mm diam. and \pm elongated in direction of axis, weakly coherent, truncate, prismatic to subprismatic, in 2 to 3 whorls. **INFLORESCENCE** green, $8\text{--}10 \times 1.2\text{--}1.5$ cm (dry); berries 3–4 mm diam. (dry).

Phenology. *Chlorospatha ilensis* is known to flower during all months except June, September, and November, with fruiting recorded for the month of August. In cultivation, *C. ilensis* flowers only periodically, with approximately one month between flowering cycles. Inflorescences emerge in slow progression, with several days between anthesis of one inflorescence and emergence of the next inflorescence at the apex of the petiole sheath.

Discussion. *Chlorospatha ilensis* is relatively widespread on the western slopes of the Andes in

central Ecuador and represents the southern limit of the genus. The northernmost collection of *C. ilensis*, which is endemic to Ecuador, was made approximately 500 km south of the southernmost collection of any other member of the section.

The species has been collected in the provinces of Azuay, Bolívar, Cotopaxi, El Oro, Los Ríos, and Pichincha at 550–1530 m elevation, most frequently in premontane wet forest, but also in tropical moist forest, premontane moist forest, and lower montane moist forest. The GPS coordinates for some collections fall in tropical dry forest, premontane dry forest, and montane dry forest in the southern provinces of El Oro and Los Ríos, where these ecological life zones predominate; however, these are presumably erroneous.

Chlorospatha ilensis is the only Ecuadorian member of *Chlorospatha* sect. *Chlorospatha* and one of only two species in the section, the latter species being *C. dodsonii*, which can have other than divided leaf blades (see discussion under *C. dodsonii*).

A number of specimens of *Chlorospatha ilensis* have previously been incorrectly determined as *C. mirabilis*, which is similar in many respects, but with notable differences, not the least of which is its distribution. *Chlorospatha mirabilis* is known only from Panama and northern and central Colombia, in Antioquia, Chocó, and Valle departments, with no collections of either species or of intermediate forms having been made in the considerable area between the known localities, although this intervening area has seen much collecting activity. The blades of *C. mirabilis* are consistently 3-lobed, usually maculate, and always more or less purple on the lower surface, thus differing from *C. ilensis* in which the blades are usually hastate, only occasionally 3-lobed, entirely green, and lack maculations. The inflorescences are sufficiently similar to indicate the sectional relationship between the species, particularly as regards the morphology of the pistils, both species having cylindrical ovaries and disklike styles. However, the ovary of *C. ilensis* is 2-locular and the style is green, whereas the ovary of *C. mirabilis* is 3- or 4-locular (possibly 5- or 6-locular) and the style is pink, pale yellow, or pale orange. The sterile staminate portion of the spadix of *C. mirabilis* is unusual in the genus in comprising ca. one third of the length of the spadix, with the sterile flowers laxly arranged in seven to nine (to 11) whorls, thus differing from that of *C. ilensis*, which occupies one tenth of the spadix or less, with the flowers densely arranged in only two or three whorls.

Plowman 14110 is unusual in the sterile state in having the petiole and sheath mostly green with some

bands of weakly darker purplish reptilian markings. When in flower, the sheath margins are broadly dark maroon and undulate (observed in cultivation at MO).

Croat 73743 is a small, sterile collection of *Chlorospatha ilensis* from Cotopaxi Province, made at 1480–1530 m elevation, well above that of the other collections (550–1010 m), most of which were made below 900 m. It differs in having fleshy petioles with free-ending sheaths, whereas those of the other collections are moderately firm and decurrent at the apex. In the course of this treatment, a sterile collection from Cañar Province was examined, *Croat 50868* (MO), which is possibly this species, but the leaf blades dry partially weakly purple-tinged on the lower surface, suggesting that the collection possibly represents *C. atropurpurea*. Cañar Province is also geographically isolated from the other provinces where *C. ilensis* has been collected.

Additional specimens examined. ECUADOR. **Azuay:** Hac. Yacopiana, on ridge bordering Río Patul, above Sanagüín, 850 m, *J. Steyermark 52802* (NY). **Bolívar:** Clementina Farms, Cerro Samana, 5.7 km S & W of main Pueblo-Viejo-Caluma rd., 5.2 km W from bridge over Río Pita (turn-off is 6.3 km E from Potosí), 371–600 m, *Croat et al. 93345* (MO, QCNE). **Cotopaxi:** along Quevedo–Latacunga rd., 55.5 km from Quevedo, 23.5 km E of La Mana, 930–950 m, *Croat 57021* (CM, MO); La Mana Cantón, along rd. betw. Guayacán (13.1 km N of La Mana) & Montinuevo (N of Pucayacu), at end of rd. branching to rt. 23.6 km from Guayacán, vic. Escuela Quindigua, 1480–1530 m, *Croat 73743* (MO, QCNE), 73772 (K, MO, QCNE); Km. 55 on Quevedo–Latacunga rd., 850–1000 m, *Dodson et al. 14409* (MO, QCNE). **El Oro:** along Machala–Loja rd., 25 km SE of rd. jct. to Piñas, 890 m, *Croat 50723* (MO); 11 km W of Piñas on rd. to Santa Rosa, 850 m, *Dodson et al. 9135* (MO, SEL, US). **Los Ríos:** along rd. E of Santo Domingo–Quevedo rd. (beginning 10.5 km N of Patricia Pilar) at Caseria Palmar de Bimbe, 550–575 m, *Croat 57003* (MO, NY, US); Quevedo Cantón, Centinela-Pirámide parish, along Santo Domingo–Quevedo rd. approaching Patricia Pilar, Km. 41, 650 m, *C. Quelal & G. Tipaz 337* (MO); Hac. Clementina, Cerro Samana, La Torre, 700–750 m, *B. Ståhl & X. Cornejo 5946* (GUAY). **Pichincha:** along old rd. to Quito from Alluriquín vía Chiriboga, 2–3 km from main Aloag–Santo Domingo de los Colorados rd., 890–1010 m, *Croat 56972* (MO); vic. Chiriboga, 900 m, *Croat 81096* (MO); 12 km W of Patricia Pilar, at Km. 45 on Santo Domingo–Quevedo rd., 600 m, *C. Dodson & D. Neill 15536* (MO, QCNE), *Dodson & Duke 7648* (SEL).

Cultivated specimens examined. ECUADOR. **El Oro:** 11 km W of Piñas on rd. to Santa Rosa, 850 m, *Plowman 14110* (F, MO, SEL, cult. from *Dodson et al. 9135*, SEL live acc. 1979–1718, cf. Fig. 26). **Pichincha:** La Centinela, 600 m, *E. Christenson 1483* (MO, cult. from type clone *Dodson et al. 7547*), *Madison s.n.* (US, cult. from type clone *Dodson et al. 7547*, SEL live acc. 79–467).

34. *Chlorospatha jaramilloi* Croat & L. P. Hannon, sp. nov. TYPE: Ecuador. Pichincha: Reserva Flor.-Ecol. Río Guajalito, Km. 59 on old Quito–

Santo Domingo de los Colorados Hwy., 3.5 km NE of hwy., foothills of Volcán Pichincha, 1800–2200 m, 0°13'53"S, 78°48'10"W, 25 Jan. 1992, *J. Jaramillo & E. Grijalva 14574* (holotype, NY!; isotype, QCA!). Figure 24B.

Herba usque ad 1 m; internodia 1.2–3.5 cm × ca. 8 mm; cataphylla 15–27.5 cm longa. Petiolus 32–68 cm longus, vaginatus per 19–40 cm; lamina foliaris ovato-sagittata, 21.5–42 × 11.5–18 cm, lobis posterioribus 8.5–18 × 5–9 cm, nervis basalibus utroque ca. 5; nervis primariis lateralibus utroque 6 vel 7. Inflorescentiae usque ad 3 in quaque axilla; pedunculus 18.5–20 cm × ca. 2 mm; spatha erecta, 9.8–11.5 cm longa, tubo ca. 5 mm diam., lamina ca. 6 cm × 6–7 mm.; spadix 6.8–9 cm longus.

Terrestrial herb, to 1 m tall; stem decumbent, with remnants of old leaf bases and cataphylls persisting ± intact along its length (all measurements made from dried material); internodes 1.2–3.5 cm × 8 mm, drying weakly glossy, dark greenish brown to reddish brown; cataphylls 15–27.5 cm long, acuminate at apex, drying weakly glossy, medium-dark to dark reddish brown. LEAVES 1 to 2, erect-spreading; **petioles** 32–68 cm long, glabrous, drying weakly glossy, medium-dark to dark reddish brown, darkest apically, sheathed 19–40 cm, slightly more than 1/2 of total length; sheath decurrent at apex; free portion 2.5–3 mm diam. midway; **blades** ovate-sagittate, 21.5–42 × 11.5–18 cm, 1.8 to 1.9 times longer than wide, abruptly acuminate at apex, weakly broadest at base, occasionally weakly narrower, 1 to 1.1 times wider at base than across anterior lobe (measured tip to tip across posterior lobes), drying thinly coriaceous, weakly bicolorous; upper surface drying matte to weakly glossy, brownish green; lower surface drying semiglossy to glossy, green; anterior lobe 15–26.5 × 12–18.5 cm, 1.2 to 1.3 times longer than wide, 1.7 to 1.8 times longer than posterior lobes, broadest below middle, ± symmetrical; posterior lobes directed toward the base, 8.5–18 × 5–9 cm, 1.6 times longer than wide, bluntly acute to narrowly rounded at apex, broadest at base or midway, or as wide midway as at base, weakly to moderately inequilateral, the inner side narrower, weakly to broadly rounded toward base, moderately to narrowly attenuate and weakly confluent with opposite lobe at base, the confluent portion obscuring petiole apex; outer side 1.5 to 1.7 times wider than inner side midway, ± straight toward base; sinus ± V-shaped, obtuse at apex; midrib and major veins round-raised on lower surface, drying raised, ± concolorous, weakly darker than surface at base; **basal veins** ca. 5 pairs, coalesced into prominent posterior rib; primary lateral veins 6 to 7 pairs, arising at 45°–65°, weakly arcuate or straight; secondary veins drying raised on

lower surface, concolorous; tertiary veins drying weakly to moderately prominulous on lower surface, weakly darker than surface; reticulate veins drying in part weakly prominulous on lower surface, otherwise distinct and flat, concolorous, occasionally in part weakly darker than surface; collective veins 3, the innermost arising from one of the lowermost lateral veins on inner side of posterior lobe, \pm parallel to and 5–7 mm from margin. INFLORESCENCES erect, to 3 per axil; peduncle held within the sheath, 18.5–20 cm \times ca. 2 mm, drying dark, blackish brown; **spathe** erect, 9.8–11.5 cm long, acuminate at apex; spathe tube purple, 3.8–5.5 cm \times ca. 5 mm, drying matte to weakly glossy, dark reddish brown on outer surface, weakly glossy to semiglossy on inner surface; spathe blade cream-colored, 6 cm \times 6–7 mm, drying matte to weakly glossy, brownish cream to pale tan on outer surface, weakly glossy to semiglossy on inner surface, marcescent, erect after anthesis; **spadix** erect, 6.8–9 cm long, sessile, adnate to spathe 2.7–4 cm at base, the entire length of pistillate portion and onto sterile staminate portion ca. 2.7 mm; pistillate portion 2.5–3.8 cm \times 2–3 mm, drying dark reddish brown; fertile staminate portion cream-colored, 3.6–4.2 cm \times 2–3 mm, bluntly acute at apex, weakly ellipsoid, drying medium reddish brown; sterile staminate portion 7–10 \times 2–3 mm, drying dark reddish brown, almost black, the axis naked ca. 1 mm at base; pistils \pm laxly arranged to weakly coherent, ca. 3 across the axis (viewed from above), 2–2.5 mm long; ovaries obtusely conical, \pm truncate at apex, 1–1.2 \times 1.5–2 mm, drying dark tan; style Type 5 (Fig. 1), ca. 1–1.2 \times 1.2–1.5 mm (attenuate portion ca. 1 mm long), the margins usually weakly coherent with those of adjacent styles; **stigma** 0.8 mm diam., prominent, truncate at apex, markedly elevated on and broader than narrowed portion of style, drying yellowish; synandria ca. 1 \times 1.5–2 mm, coherent, truncate, weakly 3- to 5-lobed, 3- to 5-androus (mostly 4), lacking microsporangia in apical 1 to 2 whorls; sterile flowers (in ca. 6 whorls) in part ca. 1 \times 1 mm in apical 2 to 3 whorls and 2- to 3-branched, the branches obtusely truncate at apex, weakly narrowed below, otherwise ca. 2 mm long, 1 \times 2–2.5 mm diam. in basal 2 to 3 whorls and elongated in direction of axis, 3- to 6-branched, the branches 1–1.3 mm long, weakly broadest at apex, coherent. Berries not known.

Phenology. Flowering is only known to occur in *Chlorospatha jaramilloi* during the months of January and February.

Discussion. *Chlorospatha jaramilloi* is known only from premontane wet forest on the western

slopes of the Andes in Pichincha Province, Ecuador, at 1800–2200 m elevation, and would be expected to occur elsewhere within the province and possibly northward into Imbabura Province. The species, a member of *Chlorospatha* sect. *Occidentales*, is characterized by its broadly sagittate leaf blades that dry matte on the upper surface and somewhat glossy on the lower surface, with the posterior lobes broad and weakly confluent at the base, the confluent portion obscuring the petiole apex. It is also distinguished by its purple spathe tube, cream-colored blade 2.5–3 cm longer than the spadix, and its 2- to 6-branched sterile flowers.

Chlorospatha jaramilloi could possibly be confused with *C. antioquiensis*, especially in the sterile state, but the latter species is known only from the northern end of the Cordillera Central in Antioquia Department, Colombia (see discussion under *C. antioquiensis*).

Chlorospatha jaramilloi is also similar to *C. bayae* from Valle Department, Colombia (see discussion under *C. bayae*).

Chlorospatha jaramilloi is most similar to *C. sagittata* from Imbabura Province, Ecuador, on the western slopes of the Andes, both having purple spathe tubes, leaf blades of similar shape and drying characteristics, and a like number of primary lateral veins (see discussion under *C. sagittata*).

Etymology. *Chlorospatha jaramilloi* is named for Jaime Jaramillo (1944–, Pontificia Universidad Católica del Ecuador), botanist, prodigious collector, and teacher, who collected the type specimen.

Paratype. ECUADOR. **Pichincha:** Res. For. La Favorita, 2.5 km from main Quito–Chiriboga–Santo Domingo rd., departing main rd. 0.7 km S of Chiriboga, 1800–1830 m, 0°12'S, 78°47'W, 15 Feb. 1992, Croat 72150 (B, K, MO, QCNE, US).

35. *Chlorospatha kolbii* Engl., Gartenflora 27: 98. 1878. TYPE: Colombia. Collected by Wallis s.n. & cultivated at Munich Botanical Garden, lost after 1879 (type, tab. 933 in Engler [1878] serves as the type [Madison, 1981]). Figures 2G–L, 28A–C.

Terrestrial herb, to ca. 50 cm tall; stem erect to 15 cm, in part subterranean, with remnants of old cataphylls persisting \pm intact and bulbils produced randomly along its length; bulbils solitary, 0.5–5 \times 4–6 mm on exposed stem, elongated below soil surface, to 5 cm \times 8 mm, weakly glossy, dark green; internodes 3–8 mm \times 1.2–1.7 cm, weakly glossy, pale-medium green, occasionally with nodes in part weakly raised and brownish with age; cataphylls 2 to

3 per leaf, (5–)10–25 cm long, obtuse with acumen or cuspidate at apex, obtusely 1-ribbed toward apex abaxially, weakly glossy, pinkish or pale-medium green, densely dark brown-, dark purplish- or black-variegated, most densely so abaxially and toward base. LEAVES 2 to 4, erect to erect-spreading; **petioles** 21.5–45 cm long, glabrous, matte, pale to medium or dark green, densely dark brownish-, purplish-, or black-variegated, less densely so toward apex, almost entirely dark brownish, purplish, or blackish toward base, minutely many-ribbed throughout, drying matte, dark brown to brownish gray, sheathed 4–20(–32) cm, 1/2 to 2/3 of total length, rarely 1/3 (ca. 1/4 of length when sterile); sheath free-ending at apex (when in flower), the margins occasionally entirely narrowly medium green; inner surface glossy, conspicuously paler; free portion 3–6 mm diam. midway, terete, obtusely 1-ribbed laterally (on both sides), acutely so to occasionally weakly alate toward apex, 1-ribbed medially; **blades** held \pm horizontally, deeply (7 to)9 to 14(15)-pedatisect, (14–)17–35.5 \times (16–)20–44 cm, 1.1 to 1.2 times wider than long, thin, moderately to conspicuously bicolorous, the margins of all segments \pm narrowly undulate; upper surface quilted, velvety, dark green to bright green, sparsely to conspicuously irregularly white-, greenish cream-, or pale yellow-green maculate, drying matte, dark green, the maculations moderately to conspicuously paler than surface, occasionally obscure; lower surface weakly glossy, weakly paler green maculate, drying weakly glossy to semiglossy, moderately paler; all segments narrowly elliptical to lanceolate or oblanceolate, moderately acuminate to long-acuminate at apex, weakly to moderately narrowed and broadly attached at base, narrowly confluent between segments, the confluent portion 2–6 mm wide; **medial lobe** 8–23.5 \times 2–3(–4.7) cm, (3.3 to)6 to 6.6 times longer than wide, occasionally equal in length to or weakly shorter than innermost lateral lobes, \pm symmetrical; **lateral lobes** 2.5–20 \times 0.6–3(–4.7) cm, (3.3 to)4.5 to 6.6 times longer than wide, progressively shorter and narrower toward outermost segments, progressively and moderately inequilateral, the inner side always narrower, most prominently so on outermost segments; outer side 1.2 to 1.6 times wider than inner side midway; outermost 1 to 2 segments markedly shorter and narrower than innermost, 3.1 to 4.4 times longer than wide; midrib and major venation deeply sunken and concolorous on upper surface, round-raised on lower surface, minutely many-ribbed and weakly granular-puberulent, weakly paler than surface, occasionally weakly purplish variegated toward base; midrib frequently entirely obtusely to acutely 1-ribbed

medially or in part only toward base on lower surface, drying weakly raised to weakly flattened, \pm concolorous, weakly darker toward base; posterior rib markedly curved, naked 3.5–6.5 cm per side, acutely 1-ribbed medially on lower surface, the rib contiguous with lateral ribs on petiole; primary lateral veins (on all segments) 2 to 4 pairs, arising at 10°–30°, weakly arcuate, drying weakly raised to weakly flattened on lower surface, \pm concolorous to weakly paler than surface, weakly darker toward base; secondary veins in part obtusely sunken on upper surface, raised or prominulous on lower surface, concolorous, drying weakly raised, concolorous; tertiary veins entirely or in part prominulous on lower surface, otherwise visible and distinct, weakly darker than surface, drying visible, distinct, \pm concolorous; reticulate veins obscure; collective veins 2 to 3, the innermost arising from lowermost lateral vein at base, loop-connected with all preceding lateral veins, frequently markedly scalloped and remote from margin (relative to blade width), 2–8 mm from margin. INFLORESCENCES erect, 4 to 8 per axil, emitting a sweet-spicy fragrance at anthesis; peduncle held within the sheath, 15–30 cm \times 2–3.5 mm, weakly broader than thick, narrowest toward base, glabrous, weakly glossy, pale yellow-green, weakly irregular darker-mottled in narrow transverse bands, drying weakly glossy to semiglossy, medium-dark green to greenish brown; **spathe** erect, (7–)8–10.5 cm long, 2.5–3.5 cm wide (flattened) toward base, lanceolate, acute or abruptly acuminate with acumen at apex (acumen ca. 1.5 mm long), \pm funnel-shaped at anthesis, the margins in-rolled in apical 2 cm; spathe tube matte to weakly glossy, medium yellow-green on outer surface, matte and weakly paler on inner surface, 4–5.5 cm \times 4–9 mm, drying weakly glossy, medium-dark greenish brown on outer surface, much paler on inner surface, sparsely pale-speckled on both surfaces; spathe blade \pm erect, matte, concolorous to weakly paler than tube, with margins paler in apical 2/3 on outer surface, matte and weakly paler on inner surface, (3–)4–5 cm \times 4–9 mm, to 2.3 cm wide (flattened), obtusely 1-ribbed abaxially, drying weakly glossy, weakly paler than tube along margins on outer surface, much paler on inner surface, opening broadly at anthesis, marcescent, erect after anthesis; **spadix** erect, stipitate 0.7–1.5 cm (stipe green, 0.5–1 mm diam.), 6–9 cm long, adnate to spathe 1–1.5(–2) cm at base, only along stipe or possibly narrowly onto pistillate portion, axis green; pistillate portion yellowish, 2–5 cm \times 4–6 mm, drying weakly pinkish brown; fertile staminate portion cream to yellowish cream, (1.6–)2.4–3.8 cm \times 3–4 mm, narrowly rounded to bluntly acute at apex,

\pm cylindrical to weakly tapering, broadest at base, occasionally weakly thicker than broad, drying pale yellow-tan; sterile staminate portion white to creamy white, \pm cylindrical or weakly to moderately tapering, (5–)9–13 \times ca. 4 mm, weakly narrower than fertile staminate and pistillate portions, drying pale tan; pistils markedly laxly arranged, 2 to 3 across the axis (viewed from above), 1.5–2 mm long; ovaries subglobose, ovoid or \pm cylindrical, white, 1.5–2 mm diam., with 2 to 3 deeply intrusive parietal placentae and subaxile placentation (pseudoaxile in basal 2/3); ovules 6 to 10 per locule, anatropous, biseriate; funicles as long as or longer than ovules; style Type 3 (Fig. 1), collar-like disk, 1.2–1.5 mm diam., with mantle to 0.5 mm thick, weakly narrower than to as broad as ovary apex, the margins not coherent with those of adjacent styles; **stigma** yellow or yellowish, 0.5–0.7 mm diam., sessile, subrounded or \pm cylindrical and obtusely truncate at apex, 3- to 4-lobed; synandria ca. 1.5 \times ca. 1.5 mm, coherent, \pm truncate, 2- to 4-lobed, 2- to 4-androus (mostly 3), occasionally lacking microsporangia in apical 1 to 2 whorls; pollen white, in tetrads, \pm ellipsoid-oblong, 30–32(–35) \times 23–25 μ m, occasionally subquadrangular and 33 \times 33 μ m, with exine variable perforated, irregularly reticulate to foveolate (Fig. 2G–L); sterile flowers in 4 to 5 whorls, 0.5–2 \times 1–1.5 mm, markedly laxly arranged, entirely \pm fungiform (like small toadstools) to 3- to 4-lobed throughout or only in apical 3 whorls and otherwise 1- to 3-branched (in basal 1 to 2 whorls), a few 1- to 2-branched and interspersed among apical 1 to 3 whorls of pistils, the branches clavate. Berries not known.

Phenology. Flowering is known to occur in *Chlorospatha kolbii* during the month of April and from July through December, and possibly occurs throughout the year. Inflorescences are fragrant and emerge in slow progression, with several days between anthesis of one inflorescence and emergence of the next inflorescence at the apex of the petiole sheath.

Discussion. *Chlorospatha kolbii* is the type species of the genus and of *Chlorospatha* sect. *Chlorospatha*. The species is known only from near sea level, in tropical wet forest on the Pacific Coast in Chocó Department, Colombia, and possibly occurs elsewhere in that department. The collections made prior to 1900 were recorded with only the country of origin, Colombia, and until recently no additional collections had been made in over 120 years. *Mora 50* is the first collection with specific locality information from a known source. Of the three modern collections, two were from Estación Biológica

El Amargal near Nuquí. The exact locality of the third collection is not known, but it is also from Chocó Department.

Chlorospatha kolbii is a strikingly beautiful species distinguished by its velvety, dark green, pale maculate, (7- to)9- to 14(to 15)-pedatisect leaf blades with long, narrow segments broadly attached and narrowly confluent at the base. The green petiole is densely dark brown-, purplish-, or almost black-mottled and sheathed one half to two thirds of its length when in flower. The species is also distinguished by its inflorescence, which can occasionally be quite large (to 10.5 cm long) for a relatively small plant, with unusual pistils and sterile flowers. The spadix is conspicuously stipitate, with the stipe to ca. 1.5 cm long, and usually adnate to the spathe only along the stipe. In most taxa with disklike styles (Type 3, Fig. 1) and sessile stigmas, the pistils are weakly coherent, but in *C. kolbii*, these are markedly laxly arranged and not at all coherent. The style itself is unusual in being collar-like as well as disklike, surrounding, but usually not coherent with the stigma. The sterile staminate portion of the spadix is also markedly laxly flowered, frequently with more than one type of sterile flower on a single spadix. The sterile flowers can be lobed (similar to the synandria), fungiform (like toadstools), or several-branched. Some of the last type is usually interspersed among the apical one to three whorls of pistils. Engler and Krause (1920) described the upper surface of the leaf blade as “scabra” and “subholosericea.” The upper surface of *Hort. Bull s.n.*, possibly a specimen from the original Wallis collection, was examined and no “hairs” were found. The surface is minutely alveolate in the dried material, which could possibly explain their use of the term “scabra,” meaning “rough to the touch.” The upper surface of the modern collections is velvety, with subhemispherical elevations, as seen under low magnification (10 \times) in both living and dried material.

Chlorospatha kolbii could be confused with only one species, *C. kressii*, known only from its type locality near Quibdó, also in Chocó Department, at 90 m elevation. The two species are remarkably similar and would be difficult to distinguish in the sterile state, although mature specimens of *C. kolbii* are significantly larger than those of *C. kressii*, with the petiole to 15 cm longer and the blades wider and as much as 10 cm longer. When in flower, the petiole of *C. kolbii* is sheathed one half to two thirds of its length and the peduncle is 15–30 cm long, thus differing from *C. kressii* with the petiole sheathed one third of its length and the peduncle 8.8–13.7 cm long. The upper surface of the leaf blade of *C. kressii*

is matte, whereas that of *C. kolbii* is velvety; however, in dried material, both have subhemispherical elevations when viewed under low magnification (10×). When *C. kressii* was published, no collections of *C. kolbii* had been made since 1878 and in delimiting the two species, Grayum (1991a) cited the difference in the number of segments (seven to nine segments in *C. kolbii* vs. 11 to 13 in *C. kressii*), with the segments narrower and longer in *C. kressii*. Recent collections of *C. kolbii* reveal that this species usually has nine to 13 or as many as 15 segments and both species have similarly shaped leaflets. Other differences mentioned by Grayum still pertain. The inflorescence of *C. kolbii* can be even larger than reported by Engler and K. Krause (1920), significantly larger than that of *C. kressii*, (7–)8–10.5 cm long versus 5–6.2 cm in *C. kressii*, and there is no purple or violet on or within the spathe or on the axis in *C. kolbii*, these structures being entirely green. Although Engler and K. Krause did not describe the blade of *C. kolbii* as maculate, there are clearly some obscure maculations on *Hort. Bull s.n.* and numerous, conspicuous maculations on all modern collections. The blade of *C. kressii* is not maculate. The habit of *C. kolbii* is erect, with some portion of the rhizome subterranean, commensurate with its short internodes (3–8 mm long). The habit of *C. kressii* is decumbent and longer internodes (8–10 mm long) accord well with this habit. Grayum did not elaborate on the morphology of the pistils in *C. kressii*, but it would appear that they, as well as the synandria and sterile flowers, are similar to those of *C. kolbii*. Only dried material of *C. kressii* was available for examination, and it is frequently difficult to discern details of flowers, particularly those of the style and stigma, which can be nearly destroyed in the drying process. It is possible that the two species will eventually prove to be conspecific; however, with so few collections presently available, it would seem best to retain the status of both until more material can be examined.

Cultivated specimens examined. COLOMBIA. s. loc., Dpto. Cult. at Hort Bull, Hort. Bull s.n., 20 Sep. 1878 (K). **Chocó:** Mpio. Nuquí, Arusí District, Est. Biol. El Amargal, sea level, 5°34'N, 77°31'W, 22 June 2000, *Croat & Mora* 83727 (AAU, B, CAS, COL, F, K, MEXU, MO, NY, SEL, TEX, US, WU) [= *Mora* 345, COL], flowered in cult., *Mora* 50 (MO); *J. Jacome s.n.* (COL); *T. Franke s.n.* (K, MO, US), flowered in cult., Munich Bot. Garden, Dec. 1995.

36. *Chlorospatha kressii* Grayum, Novon 1: 12–14. 1991. TYPE: Colombia. Chocó: ca. 10–15 km S of Quibdó, on rd. to Istmina (Pan-American Hwy.) & 8–10 km E on rd. to petroleum exploration camp, ca. 90 m, 5°35'N, 76°37'W,

9 July 1986, *M. Grayum, B. Hammel, J. Kress & G. Brown* 7643 (holotype, COL-353940 and COL-353941!; isotypes, CHOCO not seen, K!, MO!). Figure 27A, B.

Terrestrial herb, less than 50 cm tall; stem decumbent, remnants of old cataphylls persisting as reddish brown fibers at upper nodes; internodes 8–10 mm long, possibly to 2.5 cm diam. when fresh, drying 8–12 mm diam., matte, dark brown; cataphylls 3.1–11.3 cm long, apex not known, broadly to narrowly lanceolate, drying fibrous, matte to weakly glossy, dark brown to blackish brown. LEAVES 3 to 4, erect-spreading; **petioles** 25.1–30.5 cm long, glabrous, green, obscurely dark-mottled, drying weakly glossy to semiglossy, dark brown to blackish brown, sheathed 1.7–11.8 cm, ca. 1/3 of total length; sheath weakly free-ending at apex; free portion 2–3 mm diam. midway (dry), terete; **blades** deeply 11- to 13(14)-pedatisect, ca. 20–27 × 22–38 cm, thin, weakly bicolorous, the margins of all segments ± undulate; upper surface matte, green, drying matte, dark greenish brown; lower surface weakly glossy, drying ± semiglossy, brownish green, weakly to moderately paler; all segments narrowly elliptical to lanceolate or oblanceolate, gradually long-acuminate at apex, occasionally moderately acuminate, weakly to moderately narrowed at base, narrowly confluent between segments, the confluent portion 0.5–2 mm wide (dry); **medial lobe** (9.8–)15–22.1 × (0.8–)2.1–3.2 cm, ca. 7 times longer than wide, usually longer than to occasionally equal in length to innermost lateral segments, ± symmetrical; **lateral lobes** 4.9–20 × ca. 1–3 cm, 4.6 to 10 times longer than wide, progressively shorter and narrower toward outermost segments, with outermost 1 to 2 segments markedly shorter than innermost, progressively weakly to moderately inequilateral, the inner side always narrower, most prominently so on outermost segments; outer side 1 to 1.7(to 2) times wider than inner side midway; midrib and major veins sunken on upper surface, round-raised and granular-puberulent on lower surface, drying weakly raised to ± flattened, concolorous to weakly darker than surface; posterior rib markedly curved, naked 3.5–7 cm per side; primary lateral veins (on all segments) 2 to 4 pairs, arising at ca. 10°–30°, straight to weakly arcuate; secondary veins drying weakly raised on lower surface, ± concolorous; tertiary veins visible on lower surface, weakly darker than surface, drying in part distinct and weakly darker than surface; reticulate veins obscure; collective veins 3, the innermost arising from lowermost lateral vein at the base, loop-connected with all preceding lateral veins, frequently markedly scalloped and remote from

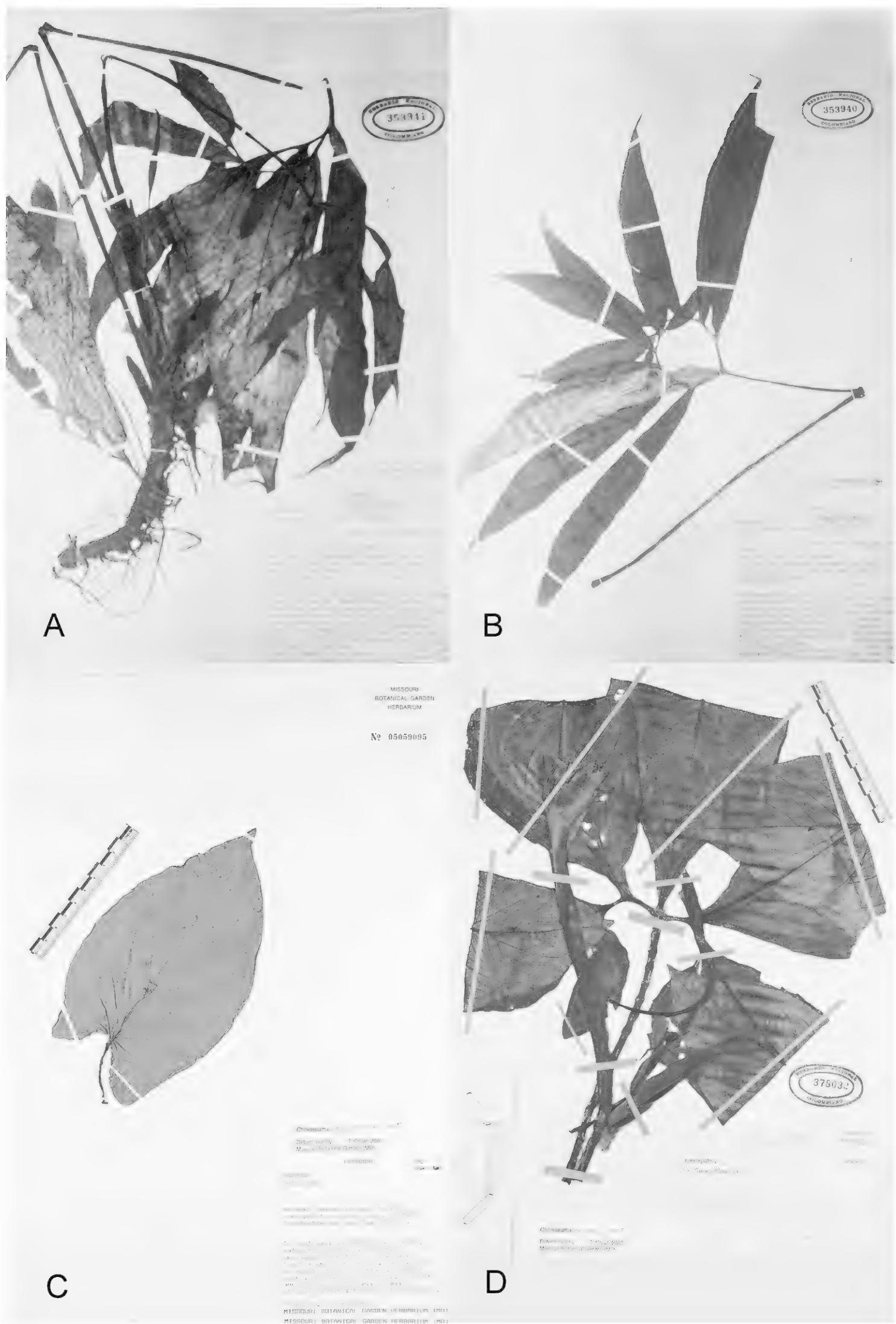


Figure 27. A, B. *Chlorospatha kressii* Grayum, specimens of the type Grayum et al. 7643 (MO). —A. Fertile holotype sheet 1 of 2 (COL-353941). —B. Sterile holotype sheet 2 of 2 (COL-353940). —C. *Chlorospatha limonensis* Croat & L. P. Hannon, the holotype Croat 78252 (MO-05059095). —D. *Chlorospatha morae* Croat & L. P. Hannon, the holotype G. Lozano et al. 6291 (COL-378032).

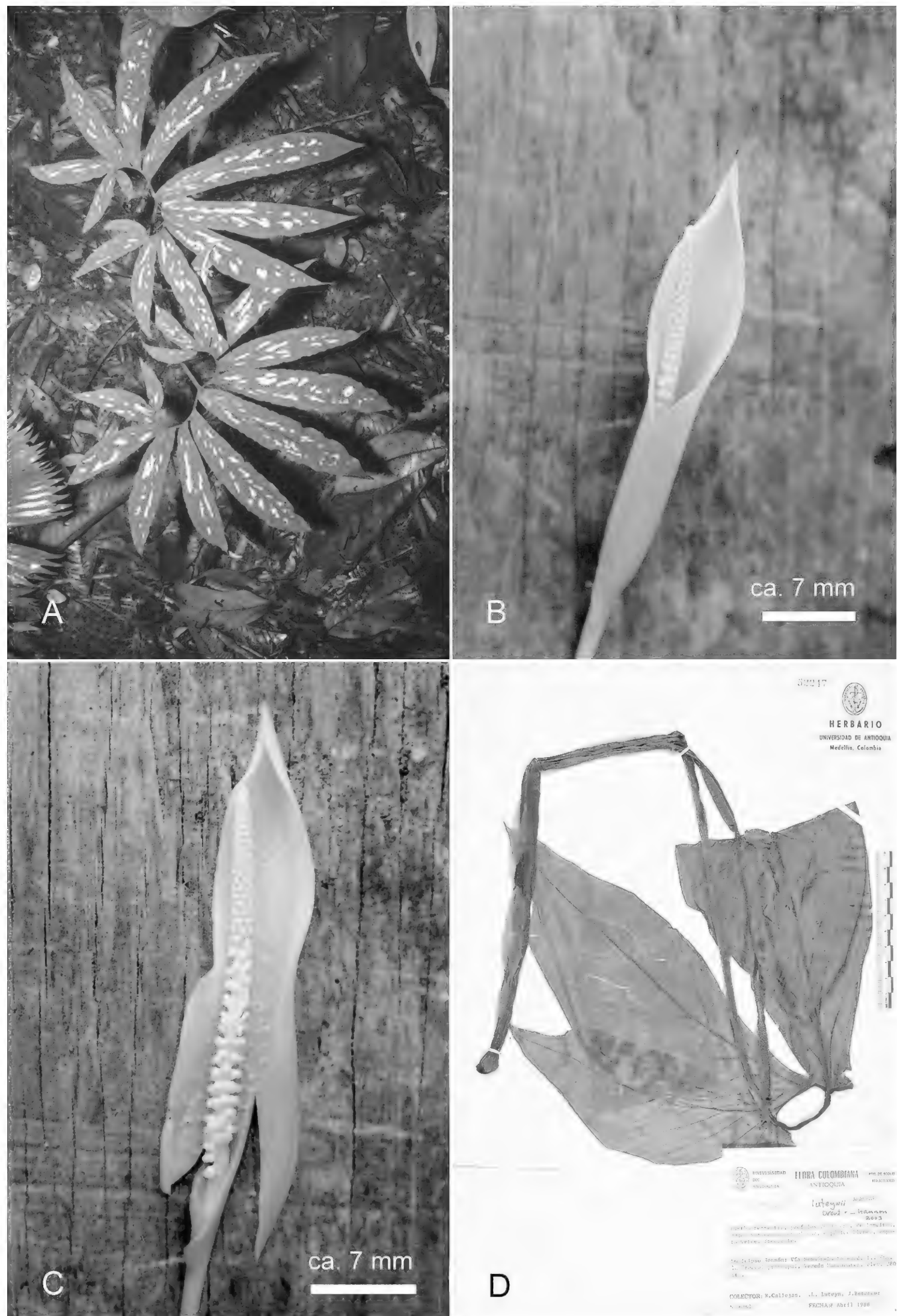


Figure 28. A–C. *Chlorospatha kolbii* Engl., photos of the collection Croat & Mora 83727 (MO). —A. Leaf blade adaxial surfaces and plant habit. —B. Inflorescence at anthesis. —C. Inflorescence at anthesis, with spathe tube cut open. —D. *Chlorospatha luteynii* Croat & L. P. Hannon, J. Luteyn & R. Callejas 11780 (HUA isotype). See also Figure 33B for the NY type.

margin (relative to blade width), 2–8 mm from margin (dry). INFLORESCENCES erect, to 4 per axil; peduncle held within the sheath, 8.8–13.7 cm \times ca. 1 mm (dry), terete, drying matte to weakly glossy, dark brown to blackish brown; **spathe** erect, uniformly green on outer surface, deep violet on inner surface in basal 3/4, pale yellow-green in apical 1/4, drying weakly glossy, medium-dark to dark brown, weakly and sparsely pale-speckled on outer surface, less so on blade, weakly paler on inner surface, with conspicuous reticulate venation when dry, 5–6.2 cm long, \pm acute at apex; spathe tube 2.7–3.2 cm \times 4–8 mm; spathe blade \pm erect, 2.3–3 cm \times 4–8 mm, marcescent, erect after anthesis; **spadix** cream-colored, erect, stipitate 5–8 mm (stipe ca. 1 mm diam. when dry), 3.9–4.2 cm long, adnate to spathe ca. 1 cm at base, only along stipe or possibly narrowly onto pistillate portion; axis violet, ca. 1 mm diam.; pistillate portion 1.7–2.2 cm long, drying ca. 2–4 mm diam., dark brownish; fertile staminate portion 1.3–1.6 cm \times 2.6–2.8 mm, bluntly acute at apex, weakly clavate or weakly broadest near base and weakly tapering, drying yellowish tan; sterile staminate portion ca. 2.5–4 \times ca. 2–2.5 mm, drying medium tan; pistils laxly arranged, 2 to 3 across the axis (viewed from above), 1.3–1.5 mm long; ovaries broadly conical, 2–2.4 mm diam., drying pale tan; style Type 3 (Fig. 1), 1–1.3 mm diam. (dry), weakly narrower than to as broad as ovary apex, the margins not coherent with those of adjacent styles; **stigma** 0.3–0.4 mm diam. (dry), sessile, obtusely truncate at apex, drying tan to dark brown; synandria ca. 1 \times 0.8–1.9 mm, coherent, \pm truncate, 2- to 3(4)-lobed, the stamens solitary or 2- to 3(4)-androus; sterile flowers 0.7–1.1 \times 0.6–0.8 mm, somewhat fungoid to \pm anvil-shaped, markedly laxly arranged. Berries not known.

Phenology. Flowering is only known to occur in *Chlorospatha kressii* during the month of July.

Discussion. *Chlorospatha kressii* is known only from the type collection made in more or less intact transitional forest between tropical wet forest and premontane rainforest on the western slopes of the Cordillera Occidental near Quibdó, in Chocó Department, Colombia, at approximately 90 m elevation. According to Grayum (1991a), the primary forest throughout the region was being actively cut when the type was collected and the only known population of *C. kressii* was probably destroyed. The label notes indicate that *C. kressii* was found on slopes near a stream. The species would be expected to occur elsewhere in Chocó, in similar habitats.

Chlorospatha kressii is a member of *Chlorospatha* sect. *Chlorospatha* and is distinguished by its small size (less than 50 cm tall) and 11- to 13(14)-pedatisect, matte, dark green leaf blades with the segments long, narrow, broadly attached at the base, and narrowly confluent between segments. There are notably few pairs of primary lateral veins (two to four) on all segments, all arising at an acute angle. The species is also distinguished by its short peduncle (to 13.7 cm long) and small inflorescence with the spathe less than 6.5 cm long and deep violet three fourths of its length on the inner surface, and the spadix cream-colored, stipitate, and adnate to the spathe only along the stipe, with the axis violet.

Chlorospatha kressii could be confused with only one species, *C. kolbii*, known only from near sea level, in tropical wet forest on the Pacific Coast in Chocó Department, Colombia, and which possibly occurs elsewhere in that department. The two species are remarkably similar and would be difficult to distinguish in the sterile state, although mature specimens of *C. kolbii* are significantly larger than those of *C. kressii*, with the petiole to 15 cm longer and the blades wider and as much as 10 cm longer (see discussion under *C. kolbii*).

37. *Chlorospatha lehmannii* (Engl.) Madison, Selbyana 5(3–4): 356. 1981. Basionym: *Caladiopsis lehmannii* Engl., Bot. Jahrb. Syst. 37: 140. 1905. TYPE: Colombia. Cauca: La Conga, W of Popayán, 1500–1800 m, *C. Lehmann* 5315 (holotype, B not seen, photo at MO!; isotypes, F!, K!). Figure 29A, B.

Terrestrial herb, less than 1 m tall; stem decumbent, erect 15 cm, remnants of old cataphylls persisting \pm intact, covering the stem (all measurements made from dried material); internodes ca. 1–1.5 \times 1.5–2.3 cm; cataphylls 15–30 cm long, acuminate at apex, acutely 1-ribbed abaxially, drying weakly glossy, medium orangish brown. LEAVES 3 to 4, erect-spreading; **petioles** 23–50 cm long, glabrous, drying matte to weakly glossy, dark brown, usually darkest basally, sheathed ca. 20 cm, ca. 1/2 or slightly more of total length (ca. 1/4 when sterile); sheath free-ending at apex; free portion 2–3 mm diam. midway; **blades** sagittate, subhastate on drying, 16–25 \times 12.5–14 cm, 1.3 to 1.8 times longer than wide, moderately acuminate to long-acuminate at apex, rarely abruptly acuminate, broadest at base, (1.7 to) 2.6 to 3 times wider at base than across anterior lobe (measured tip to tip across posterior lobes), weakly or not at all constricted in area of petiole attachment (rarely moderately constricted), coriaceous, moderately to conspicuously bicolorous; upper surface velvety, dark

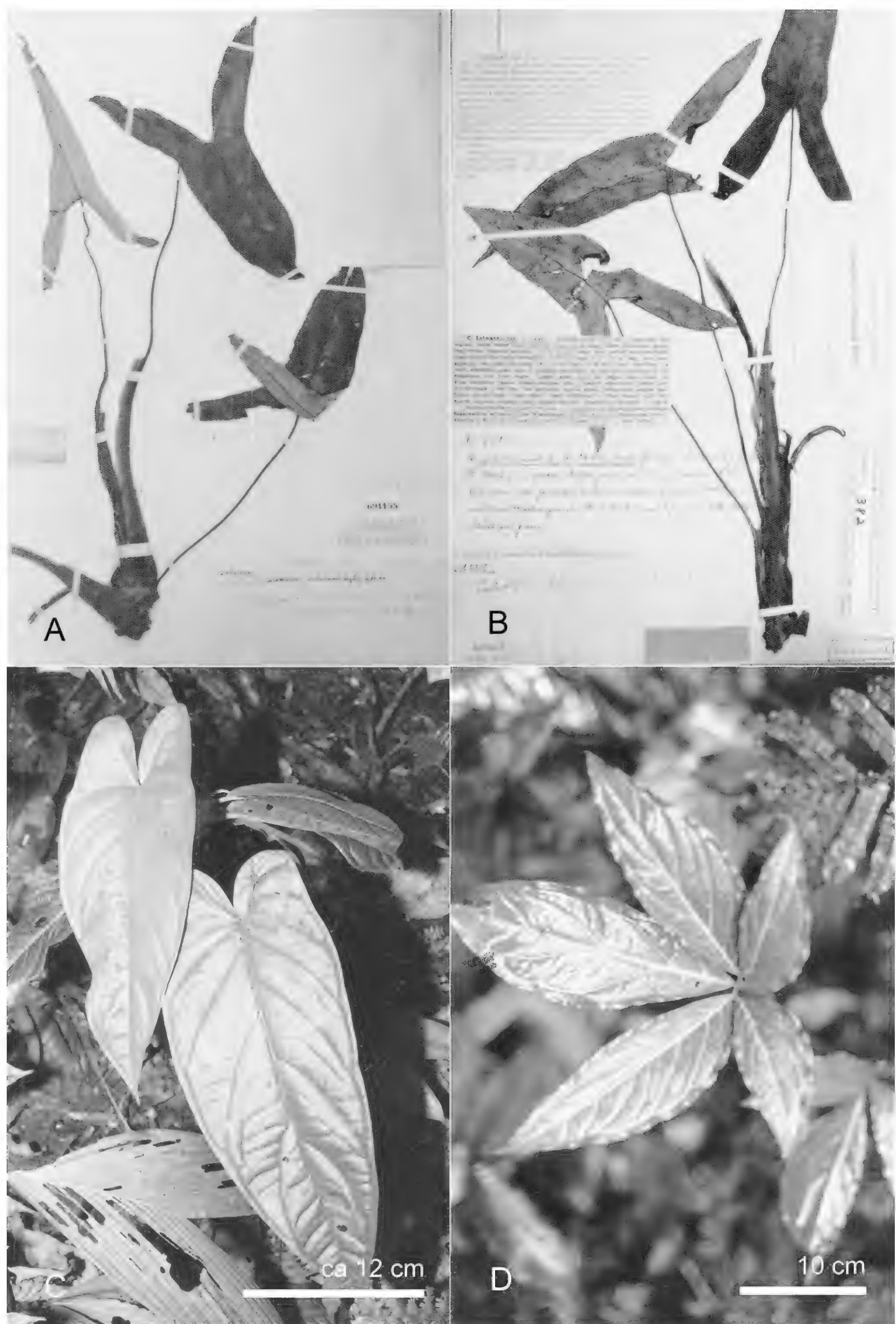


Figure 29. A, B. *Chlorospatha lehmannii* (Engl.) Madison, photos of the type collection *Lehmann 5315* (B). —A. Isotype specimen (F). —B. Holotype specimen. —C. *Chlorospatha longiloba* Croat & L. P. Hannon, photographed from the holotype *Croat et al. 82326* (MO); plant habit, showing adaxial blade surfaces. —D. *Chlorospatha morae* Croat & L. P. Hannon, photographed from the paratype collection *Croat 56303* (MO); plant habit, showing adaxial blade surfaces.

yellowish green, drying velvety-matte, dark brown, densely dark purple-brown, punctiform (speckles regularly rounded, appearing as subepidermal cellular inclusions); lower surface drying matte, moderately to conspicuously paler, narrowly dark purple-brown, punctiform (usually in single row) along major veins; anterior lobe $10.5\text{--}16 \times (3\text{--})4.5\text{--}6\text{--}(9)$ cm, (1.6 to) 1.8 to 2.8 times longer than wide, 1.4 to 1.5 times longer than posterior lobes, broadest at or near base, weakly inequilateral; posterior lobes directed toward the base, usually outward on drying, $(6\text{--})7\text{--}11 \times (1\text{--})1.5\text{--}3\text{--}(4)$ cm, usually 3.1 to 4 times longer than wide, bluntly acute at apex, broadest at or below middle, \pm symmetrical to weakly inequilateral, the inner side weakly narrower, weakly rounded to occasionally broadly rounded toward base, gradually attenuate onto posterior rib; outer side \pm straight, rarely weakly convex toward base; midrib sunken on upper surface, round-raised on lower surface, drying raised, \pm concolorous to weakly darker than surface; **basal veins** 3 to 4 pairs, coalesced into prominent posterior rib; posterior rib naked 5–7 mm per side; primary lateral veins 4 to 6 pairs, arising at $45^\circ\text{--}65^\circ\text{--}(80^\circ)$, straight or weakly arcuate, drying weakly raised near base on lower surface, otherwise flattened, moderately to prominently darker than surface; interprimary veins drying weakly raised on lower surface; secondary veins drying in part prominulous, otherwise flat on lower surface, in part weakly darker than surface; tertiary veins drying flat on lower surface, weakly darker than surface; reticulate veins drying obscure; collective veins 3, the innermost arising from one of the lowermost lateral veins on inner side of posterior lobe, \pm parallel to and ca. 5 mm from margin. **INFLORESCENCES** erect, 2 to 3 per axil; peduncle held within the sheath, $(15\text{--})20\text{--}27$ cm \times 1.5–3 mm, drying matte, dark brown; **spathe** erect, 10.5–11 cm long, acuminate at apex, drying sparsely dark purple-brown, punctiform on outer surface; spathe tube green, $4.5\text{--}6.2$ cm \times 5–10 mm, drying matte, dark brown on outer surface, \pm concolorous and dark violet-tinged in medial 1/3 on inner surface; spathe blade white, 4.5–5 cm long, drying 1.3–2 cm wide (flattened), narrowly elliptical, pale to medium tan, much paler than tube, marcescent, erect after anthesis; **spadix** 9–9.3 cm long, sessile, adnate to spathe 3.5–5 cm at base, most or all of the length of pistillate portion; pistillate portion 3.5–5 cm \times 4–5 mm, drying dark purplish brown; fertile staminate portion 3.5–3.7 cm \times 2.5–5 mm, narrowly rounded at apex, clavate or tapering, drying medium grayish brown; sterile staminate portion ca. $9 \times 2\text{--}3.5$ mm, drying medium brown; pistils laxly arranged, ca. 3 across the axis (viewed from above), ca. 2.5 mm long; ovaries subglobose to

obtusely conical, truncate at apex, ca. 1.5 mm diam., 2- to 3-locular, with 2 to 3 deeply intrusive parietal placentae and pseudoaxile placentation, drying brownish cream; ovules ca. 12 per locule (est.), hemianatropous, 3- to 4-seriate; funicles longer than ovule; style Type 7 (Fig. 1), ca. $0.7 \times 1\text{--}1.5$ mm, comprising ca. 1/2 of the length of pistil, the margins not coherent with those of adjacent styles; **stigma** ca. 0.2 mm diam., capitate, coronate, markedly elevated on and weakly broader than narrowed portion of style, drying dull, pale amber; synandria $1\text{--}1.5 \times 1\text{--}1.5$ mm, coherent, truncate, deeply 3- to 5-lobed, 3- to 5-androus; sterile flowers in 4 to 5 whorls, $1.5\text{--}2 \times$ ca. 1.5 mm, \pm fungiform (like toadstools), broadest at apex and broadly concave medially in apical 3 whorls, 2- to 5-branched in basal 1 to 2 whorls, the branches broadest and darker apically, abruptly narrowing below apex, \pm coherent. Berries not known.

Phenology. Flowering is only known to occur in *Chlorospatha lehmannii* during the month of June.

Discussion. *Chlorospatha lehmannii* is known only from two Lehmann collections made on the western slopes of the Cordillera Occidental in Cauca Department in southern Colombia, at 1500–1800 m elevation, presumably in a premontane rainforest. The label notes report the type locality as “La Conga, thick rain forest west of Popayán.” La Conga cannot be located on any map and it is possible that it no longer exists as a place name, many place names that are 100 years old or more having been completely abandoned. However, the label notes for *C. congensis* also mention La Conga and that it was situated along the banks of the Río Timbiquí, which would place the site on the western slopes of the Cordillera Occidental. The first author recently found the supposed area somewhat on the dry side, with no towns or farms, but the area could still easily support *Chlorospatha* in secluded habitats within the region.

Chlorospatha lehmannii, the type species for *Chlorospatha* sect. *Occidentales*, is a small plant distinguished by its coriaceous, velvety, dark yellowish green leaf blades that dry prominently subhastate, with the lobes narrow, particularly the posterior lobes, which are 3 to 4 times longer than wide. The posterior lobes are acute at the apex and long, relative to the length of the anterior lobe that is only 1.4 to 1.5 times longer than the posterior lobes. The upper surface of the blade dries densely dark purplish brown, punctiform, with the speckles regularly rounded, appearing as subepidermal cellular inclusions, a condition observed in only one other species. The lower blade surface dries matte-subvelvety and narrowly dark purplish brown, punctiform along the

major veins, with all but the midrib and interprimary veins flattened. It is also distinguished by its inflorescence, which is large relative to plant size, with the pistillate portion of the spadix conspicuously longer than the fertile staminate portion.

Two species from Valle Department, Colombia, at similar elevations, *Chlorospatha giraldoi* and *C. noramurphyae*, have similar blades that lack the purple speckling observed in *C. lehmannii*, and in both, the petiole sheath is proportionally longer and decurrent at the apex. The lower surface of the blade dries somewhat glossy in both species, the spathe is either red or yellow, and the sterile staminate portion of the spadix is more than 1.2 cm long. In *C. lehmannii*, the lower surface dries subvelvety, the spathe tube is green and the blade white, and the sterile portion is less than 1 cm long (see discussions under *C. giraldoi* and *C. noramurphyae*).

Madison (1981) originally filed *Madison 3988*, the type for *Chlorospatha carchiensis*, as *C. lehmannii*. *Chlorospatha carchiensis* could not be easily confused with that species and should be considered distinct. The leaf blades of *C. lehmannii* dry subhastate, subcoriaceous, and not at all constricted in the area of petiole attachment, with the upper surface velvety-matte and dark brown and the lower surface matte, with all venation except the midrib more or less flattened and darker than the surface. The blades of *C. carchiensis* dry sagittate, thin, and moderately to prominently constricted, with the upper surface matte to weakly glossy green and the lower surface semiglossy, with the major and secondary venation conspicuously raised and concolorous or slightly paler than the surface. The posterior lobes are less than 2 to 2.5 times longer than wide, whereas those of *C. lehmannii* are much narrower, 3 to 4 times longer than wide. The peduncle and spadix are proportionally longer in *C. carchiensis*, with the spadix adnate to the spathe about three fourths of the length of the pistillate portion, the pistils densely arranged, and the style (Type 9, Fig. 1) broader than the ovary apex, comprising one third of the length of the pistil, with the margins more or less coherent with those of adjacent styles. In *C. lehmannii*, the spadix is adnate to the spathe most or all of the length of the pistillate portion and pistils are laxly arranged, with the style (Type 7, Fig. 1) comprising one half of the length of the pistil and the margins not at all coherent with those of adjacent styles. The synandria of the latter species dry matte, medium grayish brown, and differ from those of *C. carchiensis*, which dry weakly glossy, medium orangish brown to dark reddish brown.

Madison (1981) also originally filed the type for *Chlorospatha grayumii* as *C. lehmannii*. *Chlorospatha*

grayumii differs from that species in significant ways and should be considered distinct. The leaf blades of *C. lehmannii* are subhastate, with the posterior lobes nearly twice as long as those of *C. grayumii*, relative to the length of the anterior lobe, and acute at the apex as opposed to narrowly rounded in *C. grayumii*, which has sagittate blades. In *C. grayumii*, the inner sides of the posterior lobes are narrowly confluent at the base, obscuring the petiole apex, differing from those of *C. lehmannii*, which are decurrent onto the posterior rib, with the rib naked 5–7 mm on each side. The blades of *C. lehmannii* dry matte on both surfaces, densely dark purplish brown, punctiform on the upper surface and moderately to conspicuously paler on the lower surface, with all orders of venation except the midrib flattened. In *C. grayumii*, the blades dry matte to semiglossy and not at all dark purplish brown, punctiform on the upper surface, and weakly glossy to semiglossy and concolorous to weakly paler on the lower surface, with the secondary and tertiary venation raised or prominulous. The latter species has six to nine pairs of primary lateral veins versus four to six pairs in *C. lehmannii*. In *C. grayumii*, the petiole is sheathed one third of its length and the inflorescence is small, with the spadix 4.2 cm long, thus differing from *C. lehmannii* in which the petiole is sheathed one half or more of its length and the inflorescence is significantly larger, with the spadix more than twice as long (9–9.3 cm long). The pistillate portion of the spadix is 3.5–5 cm long, with the pistils laxly arranged and the style approximately as wide as the ovary apex (not broadly spreading) in *C. lehmannii*. In *C. grayumii*, the pistillate portion is only 1.9 cm long, with the pistils weakly coherent and the style broadly spreading and much wider than the ovary apex. The sterile flowers of the latter species are subprismatic and laxly arranged in the basal three whorls (of six whorls), differing from *C. lehmannii*, which has densely arranged, fungiform (like toadstools), and branched sterile flowers throughout. The synandria of the latter species are 3- to 5-androus and dry medium grayish brown, whereas those of *C. grayumii* are 2- to 4-androus (mostly 3) and dry dark reddish brown.

Additional specimen examined. COLOMBIA. **Cauca:** La Conga, *C. Lehmann s.n.* (K).

38. *Chlorospatha limonensis* Croat & L. P. Hannon, sp. nov. TYPE: Ecuador. Morona-Santiago: betw. Gualaquiza & military checkpoint south of Limón, betw. Tucumbatza & San Juan Bosco, ca. 1200 m, Nov. 1995, *Croat 78252* (holotype, MO-05059095!). Figure 27C.

Herba terrestris; internodia 6–8 mm diam. Petiolus vaginatus usque ad 1 cm infra apicem; lamina foliaris ovato-elliptica, subsagittata, ca. 18.5×11 cm (6.2 cm lata ad basim), lobis posterioribus $3.5\text{--}4 \times 3.8\text{--}4$ cm, nervis basalibus utroque 5 vel 6, nervis primariis lateralibus utroque 4 vel 5. Inflorescentia 1 in quaque axilla; pedunculus ca. $25 \text{ cm} \times 3 \text{ mm}$; spathe erecta, ca. 4.6 cm longa, tubo ca. $1.4 \text{ cm} \times 5 \text{ mm}$, lamina erecta, ca. $3.2 \text{ cm} \times 4 \text{ mm}$; spadix ca. 3.7 cm longus.

Terrestrial herb; stem not known; internode length not known, 6–8 mm diam., drying matte, dark green; cataphylls drying as pale fibers (all measurements made from dried material). LEAVES 1; **petiole** total length unknown, glabrous, medium green becoming purple-violet and weakly, finely purplish striate-lineate toward apex, drying matte, dark brown, weakly purplish at apex; sheath not known; free portion ca. 1 mm diam. midway, terete, narrowly and obtusely sulcate; **blade** ovate-elliptic, subsagittate, 18.5×11 cm (6.2 cm wide at base), 1.7 times longer than wide, apiculate at apex, broadest across anterior lobe, ca. 1.8 times wider across anterior lobe than at base, subcoriaceous, conspicuously bicolorous, drying moderately bicolorous; upper surface matte, dark green, drying matte, dark green; lower surface reticulate, narrowly minutely colliculate along all venation, matte, drying matte; anterior lobe 16.2×11 cm, 1.5 times longer than wide, 4 to 4.6 times longer than posterior lobes, broadest midway; posterior lobes directed toward the base, $3.5\text{--}4 \times 3.8\text{--}4$ cm, about as long as wide, narrowly to bluntly rounded at apex, broadest at base, markedly inequilateral, the inner side narrower, acute to weakly rounded toward the base and decurrent onto petiole; outer side ca. 5 times wider than inner side midway, weakly concave toward the base; midrib and major veins convex on lower surface, drying raised, weakly darker than surface; midrib bluntly angular on upper surface, weakly paler than surface; **basal veins** 5 to 6, coalesced into short posterior rib ca. 1 cm long, 3 acroscopic, 2 to 3 basiscopic, the first free to the base, second and third fused near the base; primary lateral veins 4 to 5 pairs, arising at $25^\circ\text{--}45^\circ$, most acutely toward apex, weakly arcuate, etched-sunken on upper surface; secondary veins weakly raised on lower surface, drying raised, concolorous; tertiary veins weakly raised on lower surface, drying in part raised, otherwise prominulous, concolorous; reticulate veins drying visible, distinct, in part prominulous, otherwise flat on lower surface, darker than surface; collective veins 3, the innermost arising from lowermost lateral vein on inner side of posterior lobe, loop-connected with all preceding lateral veins, markedly scalloped and remote from margin (relative to blade size), 5–10 mm from margin. INFLORESCENCE (description of dimensions of

inflorescence and flowers made from pickled material and label notes) erect, 1 per axil; peduncle possibly held within the sheath, $25 \text{ cm} \times 3 \text{ mm}$, weakly purple-tinged green; **spathe** erect, weakly glossy, medium green, 4.6 cm long, lanceolate, acuminate at apex; spathe tube $1.4 \text{ cm} \times 5 \text{ mm}$; spathe blade erect, $3.2 \text{ cm} \times 4 \text{ mm}$, obtusely 1-ribbed abaxially, reflexing after anthesis; **spadix** erect, 3.7 cm long, sessile, adnate to spathe 8 mm at base, $2/3$ of the length of pistillate portion; pistillate portion $1.2 \text{ cm} \times 2.5 \text{ mm}$, broadest midway, the axis naked in basal 2 mm; fertile staminate portion dark purple-violet, $2.2 \text{ cm} \times 1.5\text{--}3 \text{ mm}$, bluntly acute at apex, tapering; sterile staminate portion $3 \times 1.5\text{--}2 \text{ mm}$, broadest at apex, the axis naked 0.5–0.8 mm at base; pistils \pm laxly arranged, 3 to 4 across the axis (viewed from above), ca. 1 mm long, \pm coherent laterally, less so between whorls; ovaries \pm cylindrical to obtusely obconical, 1–1.5 mm diam., obtusely truncate at apex, 2-locular with axile placentation, rarely 1-locular with subaxile placentation; ovules 6 to 10 per locule, hemianatropous, 2- to 3-seriate; funicles shorter than ovules; style Type 1 (Fig. 1), 1–1.5 mm diam., as broad as ovary apex, the margins conspicuous, not coherent with those of adjacent styles; **stigma** ca. 0.25 mm diam., sessile, cylindrical; synandria 6 to 7 per spiral, ca. $1 \times 2 \text{ mm}$, coherent, deeply (2)3- to 4-lobed, to the middle or occasionally nearly so, truncate or with the lobes weakly thickened in apical 2 to 3 whorls, (2)3- to 4-androus (mostly 3), the margins weakly sinuate; sterile flowers ca. 1 mm long, $1.3\text{--}1.5 \times 1\text{--}1.1 \text{ mm}$ diam. and \pm elongated in direction of axis, coherent, truncate, irregularly prismatic, with numerous minute red chromoplasts, in 3 whorls. Berries not known.

Phenology. Flowering is only known to occur in *Chlorospatha limonensis* during mid-June, the species having been collected in the sterile state in the month of November and later flowering in cultivation. *Chlorospatha limonensis* is one of only three species in which the spathe is known to reflex after anthesis and one of only five species from the eastern slopes with synandria that are truncate at the apex. The species is unique among those from the eastern slopes in having the fertile staminate portion of the spadix dark purple-violet, this portion being white to cream-colored and occasionally weakly greenish to yellowish-tinged (rarely yellow) in all others.

Etymology. *Chlorospatha limonensis* is named for the town of Limón, Ecuador, in Morona-Santiago Province, near which the type was collected.

Discussion. *Chlorospatha limonensis* is known only from the type collection made in Morona-

Santiago Province, Ecuador, between Gualaquiza and the military checkpoint south of Limón, between Tucumbatza and San Juan Bosco, in premontane moist forest on the eastern slopes of the Andes at approximately 1200 m elevation. The species would be expected to occur elsewhere within the province, southward into Zamora-Chinchipe Province, and possibly eastward into Peru.

Chlorospatha limonensis is represented by a single, incomplete herbarium specimen and pickled inflorescence; therefore, much of the description of the living plant comes from extensive label notes. The species is a member of *Chlorospatha* sect. *Orientales* and is distinguished by its subcoriaceous, ovate-elliptic, subsagittate leaf blades that are matte on both surfaces, with the upper surface dark green and the lower surface reticulate and conspicuously paler. The upper surface is flat (not quilted), with the midrib and major venation etched-sunken. The midrib is noteworthy, possibly unique in the genus, in being bluntly angular on the upper surface, the midrib usually being flat and featureless in *Chlorospatha*. The species is also distinguished by its medium green petiole that is finely purplish striate-lineate toward the apex and long, purple-tinged peduncle (25 cm long), the longest recorded for a species from the eastern slopes of the Andes. The inflorescence of *C. limonensis* is small (4.6 cm long), with the spathe entirely medium green and the spadix adnate to the spathe two thirds of the length of the pistillate portion, a greater portion of the length than in any other species from the eastern slopes in Ecuador, except *C. sucumbensis*.

Chlorospatha limonensis could possibly be confused with *C. longipoda*, which is widespread on the eastern slopes of the Andes in Ecuador, at 470–1700 m elevation, and is possibly sympatric with *C. limonensis* in Morona-Santiago Province. The species could be confused only in the sterile state. Both species have leaf blades that are usually narrower at the base than across the anterior lobes, but the blades of *C. limonensis* are subcoriaceous and more or less flat on the upper surface, with the midrib and major veins etched-sunken, differing from those of *C. longipoda*, which are quilted on the upper surface and thin to thinly coriaceous, with the midrib and major veins deeply sunken. The petioles of *C. longipoda* are green, usually not at all purplish, and not striate-lineate as they are in *C. limonensis*. In the latter species, the peduncle is 25 cm long versus 4–10 cm long in *C. longipoda*. The spadix of *C. limonensis* is adnate to the spathe two thirds of the length of the pistillate portion, with the fertile staminate portion tapering and dark purple-violet

and the synandria truncate at the apex. *Chlorospatha longipoda* differs in having the spadix adnate one half of the length or less of the pistillate portion, with the fertile staminate portion more or less cylindrical and whitish or green, yellow-green to yellow-tinged white, and the synandria broadly concave medially with the lobes prominently thickened. The ovaries of the latter species are 2- or 3-locular versus (1)2-locular in *C. limonensis*.

39. *Chlorospatha litensis* Croat & L. P. Hannon, sp. nov. TYPE: Ecuador. Esmeraldas: Lita–San Lorenzo rd., 14.2 km W of old Río Lita bridge (below Lita, prior to 1999), 425 m, 0°52'11"N, 78°27'16"W, 4 July 1998, Croat, L. P. Hannon, D. Mansell & J. Whitehill 82311 (holotype, MO-04889302!; isotypes, B!, K!, NY!, QCNE!, US!). Figure 30A–D.

Herba usque ad 1.5 m; internodia 1–3 × 2–3.5 cm; cataphylla 15–28 cm longa. Petiolus 35–70 cm longus, vaginatus per (25–)32–60 cm; lamina foliaris hastata, 17–33 × 23–36 cm, lobis posterioribus (11–)14–21 × 4.5–6.2 cm, nervis basalibus (6)7, nervis primariis lateralibus utroque (7)8 ad 10(11). Inflorescentiae 3 in quaque axilla; pedunculus 37–62 cm × ca. 2 mm; spatha erecta, 8.8–12 cm longa, tubo 3–5 mm diam., lamina 6–8.5 cm × ca. 6 mm; spadix 8.2–9.5 cm longus.

Terrestrial herb, to 1.5 m tall; stem decumbent, with remnants of old cataphylls persisting ± intact at upper nodes, otherwise as short linear fibers; sap milky; internodes 1–3 × 2–3.5 cm, matte to weakly glossy, dark green to gray-green, drying matte, medium-dark to dark reddish brown (most measurements made from dried material); cataphylls 15–28 cm long, moderately thick, obtuse at apex, with subapical apiculum (apiculum to 1.3 cm long), prominently obtusely 1-ribbed and matte, medium yellow-green on outer surface, glossy and paler on inner surface, drying weakly glossy, dark reddish brown. LEAVES 2 to 6, erect-spreading; **petioles** 35–70 cm long, moderately firm, glabrous, matte, markedly dark green, rarely purplish brown toward base and yellow-green at apex, drying matte, medium-dark reddish brown, sheathed (25–)32–60 cm, ca. 3/4 or more of total length (1/2 to 2/3 when sterile); sheath free-ending at apex, the sides rarely prominently narrowly undulate; free portion 2.5–6 mm diam. midway, finely and obtusely many-ribbed abaxially in apical 4 cm or more, sharply D-shaped or U-shaped, with margins erect and acute most or all of its length, rarely terete or subterete, obtusely 1-ribbed medially, occasionally obtusely sulcate near apex; **blades** held ± horizontally, hastate to markedly hastate, 17–33 × 23–36 cm, 1.1 to 1.3 times wider than long, weakly



Figure 30. A, B. *Chlorospatha litensis* Croat & L. P. Hannon, photos from the paratype collection *Croat et al.* 82512 (MO). —A. Fertile habit. —B. Closer view of the leaf blade adaxial surface. C, D. Photos of the holotype *Croat et al.* 82311 (MO). —C. Fertile plants lying on floor. —D. Closer view, showing the leaf blade abaxial surface. Note the post-anthesal inflorescence at center.

acuminate at apex, broadest at base, 2.4 to 2.6(to 3.5) times wider at base than across anterior lobe (measured tip to tip across posterior lobes), thin to thinly coriaceous, weakly to moderately bicolorous; upper surface usually \pm corrugate, weakly glossy to matte-subvelvety (rarely glossy), dark green, drying weakly glossy, dark blackish brown or reddish brown, rarely medium-dark olive-brown; lower surface weakly glossy to semiglossy (rarely matte), drying semiglossy, weakly paler; anterior lobe $15\text{--}30 \times 7\text{--}15$ cm, 1.8 to 2.4 times longer than wide, 1.1 to 1.6 times longer than posterior lobes, broadest at or below middle, moderately to markedly constricted at base, \pm symmetrical to weakly inequilateral; posterior lobes directed prominently outward, $(11\text{--})14\text{--}21 \times 4.5\text{--}6.2$ cm, (2.4 to)2.8 to 4.2 times longer than wide, acute to weakly acuminate at apex, broadest at or below middle, markedly constricted at base, weakly to moderately inequilateral, the outer side narrower, \pm straight toward the base; inner side 1.1 to 1.5(to 2.1) times wider than outer side midway, weakly rounded toward the base and gradually to abruptly attenuate onto posterior rib; midrib and major veins prominently narrowly sunken on upper surface, round-raised on lower surface, minutely obtusely many-ribbed, glabrous, matte, weakly darker than surface, rarely weakly paler, drying \pm raised, in part weakly flattened; midrib concolorous on upper surface, rarely weakly paler, drying concolorous to weakly darker than lower surface; **basal veins** (6)7 pairs, coalesced into prominent posterior rib; posterior rib naked 0.5–2 cm per side, acutely 1-ribbed medially on lower surface, the rib contiguous with acute margins of petiole; primary lateral veins (7)8 to 10(11) pairs, arising at $30^\circ\text{--}50^\circ\text{--}(65^\circ)$, most acutely toward apex, \pm straight to weakly or moderately arcuate, drying concolorous to weakly darker than lower surface; secondary veins obtusely sunken on upper surface, raised on lower surface, drying raised, concolorous to weakly darker than surface; tertiary veins in part obtusely sunken on upper surface, in part raised on lower surface, otherwise flat, distinct, and darker than surface, drying in part \pm prominulous to weakly raised, otherwise flat and distinct, concolorous to weakly darker than surface; reticulate veins mostly obscure, occasionally in part weakly prominulous on lower surface, concolorous, drying \pm obscure, occasionally in part weakly prominulous; collective veins 3, the innermost arising from lowermost lateral vein on inner side of posterior lobe, loop-connected with all preceding lateral veins, \pm parallel to and 2–7 mm from margin. INFLORESCENCES erect, to 3 per axil, emitting a sweet fragrance at anthesis; peduncle held within the sheath, $37\text{--}62$ cm \times ca. 2 mm, weakly

shorter to weakly longer than petiole, pale green, drying weakly glossy, dark brown (rarely tan); **spathe** erect, 8.8–12 cm long, occasionally to 3.5 cm longer than spadix, acuminate or cuspidate at apex; spathe tube matte, pale yellow-green on outer surface, glossy on inner surface, $3\text{--}3.5$ cm \times 3–5 mm, drying matte, dark reddish brown to blackish brown on outer surface, weakly glossy on inner surface; spathe blade matte, white to greenish white or pale yellow-green on outer surface, glossy on inner surface, $6\text{--}8.5$ cm \times ca. 6 mm, drying matte, pale tan to medium-dark brown or reddish brown on outer surface, marcescent, erect after anthesis; **spadix** erect, weakly stipitate 1–3 mm, 8.2–9.5 cm long, adnate to spathe 1.5–2.5 cm at base, along stipe and ca. $2/3$ to $3/4$ of the length of pistillate portion; pistillate portion bright orange, rarely white (pinkish to pale orange pre-anthesis), $2.2\text{--}3.5$ cm \times 2–4 mm, wider than thick, broadest midway; fertile staminate portion bright orange, $3.8\text{--}4.2$ cm \times 3.5–5 mm, bluntly acute at apex, tapering, broadest just above the base, drying dark, reddish brown; sterile staminate portion (probably cream-colored), $(1\text{--})1.5\text{--}2.5$ cm \times 2–3 mm, usually with axis naked between whorls and to 1 cm at base, rarely flowered entire length, drying brownish cream to medium brown; pistils weakly coherent (more laxly arranged in basal whorls), ca. 4 across the axis (viewed from above), ca. 1.5 mm long; ovaries subglobose, 1.2–2 mm diam., drying \pm tan; style Type 6 (Fig. 1), ca. $0.5 \times 1.2\text{--}2$ mm, comprising ca. $1/3$ of the length of pistil, the margins \pm coherent with those of adjacent styles, drying red-brownish cream; **stigma** ca. 0.2–0.3 mm diam., weakly elevated on and weakly broader than narrowed portion of style, drying medium to dark red-brown; synandria $1\text{--}1.5 \times 1.1\text{--}2.5$ mm, coherent, truncate, deeply (2)3- to 4-lobed, (2)3- to 4-androus, drying dark red-brown; sterile flowers less than 1 mm long, usually 1 mm \times 1.5–3 mm diam. and \pm elongated in direction of axis (rarely ca. 1 mm diam. and not elongated), coherent, truncate, subprismatic, laxly arranged in 5 to 7 whorls. INFRUCTESCENCE drying 6.7×1.1 cm, weakly glossy, dark reddish brown on both surfaces; berries drying 2.5–3 mm diam., pale to medium tan.

Phenology. Flowering in *Chlorospatha litensis* is only known to occur during the months of July and December. Inflorescences emerge in slow progression, with several days between anthesis of one inflorescence and emergence of the next inflorescence at the apex of the petiole sheath.

Etymology. *Chlorospatha litensis* is named for the town of Lita, in Esmeraldas Province, Ecuador, near

the type locality and the border of Carchi and Imbabura provinces.

Discussion. *Chlorospatha litensis* is known from premontane wet forest and lower montane rainforest in the Lita–San Lorenzo region of Esmeraldas Province in northwestern Ecuador, at 350–425 m elevation, and from premontane wet forest and premontane rainforest in Nariño Department in southern Colombia, at 1100–1325 m elevation. All collections were made in the frontier region on the Pacific slopes, along the border between the two countries. The species is a member of *Chlorospatha* sect. *Occidentales* and is distinguished by its usually corrugate, hastate leaf blades and finely ribbed, long-sheathed petiole with the sheath free-ending at the apex and the free portion usually sharply D-shaped, with erect, acute margins. The petiole is sheathed three fourths to almost its entire length, commensurate with its unusually long peduncle that is usually nearly as long as or longer than the petiole, an unusual condition in *Chlorospatha*. The midrib and major veins on the lower surface are finely ribbed and usually darker than the surface. *Chlorospatha litensis* is one of only five species in the genus with bright orange synandria, all of which occur in the frontier region and are possibly closely related. The sterile staminate portion of the spadix of *C. litensis* is unusually long relative to total spadix length, frequently nearly as long as the pistillate portion.

Chlorospatha litensis would be most easily confused with *C. dodsonii*, with which it is sympatric in the Lita–San Lorenzo region of Esmeraldas Province (see discussion under *C. dodsonii*).

In one collection from Esmeraldas, *Madison 6947*, the style is reported as white, differing from the characteristic orange color observed in *Chlorospatha litensis*. *Croat et al. 82512* (its fertile habit seen in Fig. 30A) records the style as pink prior to anthesis. It is common for style color to intensify as it develops toward anthesis, and this possibly explains the discrepancy noted here. The floral characters are otherwise identical. With so few collections available, it is impossible to draw a definite conclusion in this regard. *Croat et al. 82512* also reports the petiole as terete rather than typically D-shaped. The fertile staminate portion of the spadix is reported as whitish in *Croat 87549*, but its dried color is identical to that of the type.

Tipaz et al. 2110 (MO, QCNE), from the Reserva Indígena Awá in Esmeraldas Province in northwestern Ecuador, is possibly this species. It differs in having a purple peduncle and grayish green-drying leaf blades. The small infructescence (5 cm long) would accord with the small inflorescence of

Chlorospatha litensis, but the synandria are reported as cream-colored, differing from the bright orange color found in *C. litensis*. Only berries were available for examination; therefore, a complete assessment of the stylar morphology was not possible.

Paratypes. COLOMBIA. **Nariño:** vic. Palmar, valley of Río Imbí, 3 km NW of Ricaurte (along Pasto–Tumaco rd.), ca. 1 km E of Texas Gulf Pipeline Maintenance Station, along slopes above Río Imbí, 1100 m, 1°08'N, 77°56'W, 14 Mar. 1990, *Croat 71456* (K, MO); Mpio. Barbacoas, Altaquer region, vic. El Barro, Res. Nat. Río Nambí, lt. bank of Río Nambí, 1325 m, 1°18'N, 78°08'W, 9 Dec. 1993, *P. Franco 5097* (COL), 11 Dec. 1993, *P. Franco 5148* (COL). ECUADOR. **Esmeraldas:** Lita–San Lorenzo rd., 0.9 km E of El Durango, 19.8 km W of Alto Tambo, 350 m, 0°52'N, 78°27'06''W, July 1998, *Croat, R. Mansell, L. P. Hannon & J. Whitehill 82512* (CAS, MO, QCNE); along Río Bogotá, Awá Commun., Bogotá, 3 km SW of main Lita–San Lorenzo Hwy., 11.5 km NW of Alto Tambo, 0°58'57''N, 78°35'58''W, 16 Sep. 2002, *Croat 87549* (B, K, MO, QCNE, US).

Cultivated specimen examined. ECUADOR. **Esmeraldas:** vic. Lita, *M. Madison 6947* (SEL).

40. *Chlorospatha longiloba* Croat & L. P. Hannon, sp. nov. TYPE: Ecuador. Esmeraldas: Lita–San Lorenzo rd., 14.2 km W of old Río Lita bridge (below Lita, prior to 1999), 425 m, 0°52'11''N, 78°27'16''W, July 1998, *Croat, L. P. Hannon, D. Mansell & J. Whitehill 82326* (holotype, MO-04889288!; isotypes, AAU!, B!, CAS!, CM!, CUVCI!, FI!, GB!, K!, MEXU!, NY!, QCNE!, S!, SEL!, TEX!, US!). Figures 29C, 31A–D.

Herba terrestris minus quam 1 m, vel saepe hemiepiphytica et 1–4 m; internodia 1–6 × 0.6–2.5 cm; cataphylla 12–24 cm longa. Petiolus 20–57 cm longus, vaginatus per 6–23 cm; lamina foliaris oblongo-elliptica, sagittata, interdum subsagittata, 20–40 × 6.3–16 cm, lobis posterioribus 3.2–13.5 × 2.3–5.5 cm, nervis basalibus utroque (2)3 ad 5, nervis primariis lateralibus utroque 5 vel 6. Inflorescentiae 2 ad 5 in quaque axilla; pedunculus 12–25 cm × 2–4 mm; spatha erecta, 5–8 cm × 4–5 mm; spadix 3.2–5.7 cm longus.

Terrestrial herb, less than 1 m tall, or frequently hemiepiphytic and 1–4 m tall; stem decumbent, remnants of old leaf bases and cataphylls persisting ± intact along its length; internodes 1–6 × 0.6–2.5 cm, glossy, medium green, drying matte to weakly glossy, dark brown; sap milky (all measurements made from dried material); cataphylls 12–24 cm long, obtuse with acumen at apex, 1-ribbed abaxially, green, drying semiglossy to glossy, medium to dark reddish brown on outer surface, weakly glossy on inner surface. LEAVES 2 to 5, erect-spreading, occasionally ± spreading; **petioles** 20–57 cm long, glabrous, weakly glossy to semiglossy, dark green,



Figure 31. *Chlorospatha longiloba* Croat & L. P. Hannon. —A. Leaf blade adaxial surfaces. —B. Fertile habit, with inflorescence visible at image bottom. —C. Stem bases with persistent cataphylls and petioles. —D. Anthesal inflorescence with erect, funnel-shaped spathe. Photos of the holotype *Croat et al.* 82326 (MO).

drying matte to weakly glossy, medium-dark to dark reddish brown, frequently with the epidermis in part separated and semiglossy to glossy, sheathed 6–23 cm, slightly less than 1/2 of total length; sheath decurrent at apex; free portion 3–5 mm diam. midway, terete or subterete; **blades** oblong-elliptic, sagittate, occasionally subsagittate, $20\text{--}40 \times 6.3\text{--}16$ cm, (2.4 to) 2.6 to 3.4(to 4) times longer than wide, gradually acuminate at apex, rarely abruptly acuminate, weakly broadest at base, occasionally 2.2 to 2.5 times wider across anterior lobe than at base (measured tip to tip across posterior lobes), weakly or not at all constricted in area of petiole attachment, thinly coriaceous, rarely thin, weakly to moderately bicolorous; upper surface weakly glossy, dark green, drying weakly glossy to semiglossy, dark green to olive-green, rarely brownish yellow-green; lower surface weakly glossy to semiglossy, drying weakly glossy to semiglossy, weakly to moderately paler; anterior lobe $17.5\text{--}31 \times 6.3\text{--}14.5$ cm, (2.1 to) 2.6 to 3.3 times longer than wide, (2 to) 2.3 to 5.4(to 6.4) times longer than posterior lobes, broadest at or below middle, \pm symmetrical to weakly inequilateral; posterior lobes directed toward the base, $3.2\text{--}13.5 \times 2.3\text{--}5.5$ cm, (1.4 to) 2 to 3 times longer than wide, narrowly rounded to bluntly rounded at apex, rarely bluntly acute, broadest at base, moderately to markedly inequilateral, the inner side narrower, \pm rounded toward the base, briefly attenuate and weakly confluent with opposite lobe, the confluent portion obscuring petiole apex; outer side 1.5 to 3 times wider than inner side midway, weakly convex to \pm straight toward the base, occasionally weakly concave; midrib deeply and narrowly sunken on upper surface, narrowly raised or round-raised on lower surface, paler than surface, drying \pm raised, weakly to moderately darker than surface, occasionally concolorous; **basal veins** (2) 3 to 5 pairs, coalesced into prominent posterior rib; primary lateral veins 5 to 6 pairs, arising at $45^\circ\text{--}65^\circ(-70^\circ)$, most acutely toward apex, weakly to moderately arcuate, occasionally strongly arcuate, etched to obtusely sunken on upper surface, acutely raised to convex on lower surface, paler than surface, drying \pm flattened, concolorous to weakly darker than surface; secondary veins etched on upper surface, weakly raised on lower surface, drying weakly raised, \pm concolorous; tertiary veins distinct, in part prominent, otherwise flat on lower surface, drying visible, distinct, in part weakly prominent, \pm concolorous; reticulate veins obscure; collective veins 3, arising from one of the lowermost lateral veins on inner side of posterior lobe, loop-connected with all preceding lateral veins, \pm parallel to and 2–7 mm from margin.

INFLORESCENCES erect to erect-spreading, 2 to 5 per axil, emitting a sweet fragrance at anthesis; sympodium held within a sympodial cataphyll; sympodial cataphyll $11\text{--}19.5 \times 1\text{--}1.5$ cm, pale to medium green, drying weakly glossy to semiglossy, pale to medium reddish brown; peduncle $12\text{--}25 \times 2\text{--}4$ mm, cylindroid, thicker than broad, broadest toward base, glossy, medium green, drying weakly glossy to semiglossy, medium to medium-dark reddish brown; **spathe** erect, 5–8 cm long, lanceolate, acute to acuminate at apex, opening narrowly most of its length and \pm funnel-shaped at anthesis, more broadly on blade, the margins directed forward; spathe tube weakly glossy, medium green and prominently dark purple-tinged, or narrowly dark purple on outer margin of outer surface, dark purple on inner surface, $2\text{--}3.5 \times 4\text{--}5$ mm, drying matte to weakly glossy or semiglossy, dark reddish brown (rarely dark green), occasionally much paler near base on both surfaces, frequently weakly purplish on inner surface; spathe blade weakly glossy, pale green to greenish white on both surfaces and frequently narrowly dark purple on outer margin toward the base on outer surface, $3\text{--}4(-4.5) \times 4\text{--}6$ mm, to 3.5 cm wide (flattened), opening \pm broadly at anthesis, drying matte to weakly glossy, medium-dark reddish brown on outer surface, rarely brownish cream, weakly to moderately paler on inner surface, marcescent, erect after anthesis; **spadix** \pm erect, curved weakly forward, 3.2–5.7 cm long, sessile, adnate to spathe 0.7–1.8 cm at base, ca. 1/2 or slightly more of the length of pistillate portion; pistillate portion creamy white to pale green or pale yellow-green, $1.5\text{--}3 \times 3\text{--}5$ mm, broadest toward apex; fertile staminate portion white to creamy white or greenish white, $1.3\text{--}2.5 \times 3\text{--}6$ mm, \pm cylindrical to weakly tapering, narrowly to bluntly rounded at apex, drying medium reddish brown, rarely brownish cream; sterile staminate portion pink or bright orange, $6\text{--}9 \times 3\text{--}5$ mm, \pm cylindrical, drying medium orangish brown or medium to dark purplish brown; (floral characters from living and pickled material) pistils weakly coherent, 3 to 4 across the axis (viewed from above), 1.5–2 mm long; ovaries \pm cylindrical, obtusely truncate at apex, ca. $1 \times 1.8\text{--}2$ mm, drying cream-colored with prominently darker veins, 2- to 3-locular, with axile placentation; ovules 8 to 14 per locule, small, hemianatropous, biseriate; funicles longer than ovules; style Type 5 (Fig. 1), $0.5\text{--}1 \times 2\text{--}2.6$ mm, comprising ca. 1/2 of the length of pistil, the margins usually coherent with those of adjacent styles, drying dark purplish brown, rarely pale tan; **stigma** disklike, ca. $0.3 \times \text{ca. } 0.5\text{--}0.7$ mm, elevated on and as wide as or weakly wider than

narrowed portion of style, drying weakly paler than style; synandria $1.5\text{--}2 \times 1.5\text{--}2$ mm, coherent, truncate, 3- to 4-lobed, 3- to 4-androus (mostly 3), drying medium to dark reddish brown, rarely brownish cream; sterile flowers ca. $1.5 \times 1.5\text{--}2.4$ mm, weakly elongated in direction of axis, coherent in apical whorls, weakly coherent to laxly arranged in basal whorls, \pm fungiform (like toadstools), subprismatic when viewed from above, broadest and weakly convex at apex, abruptly narrowed below, the narrowed portion ca. 0.8 mm diam., in 6 to 8 whorls. INFRUDESCENCE (immature) $3.5\text{--}5.5$ cm \times ca. 7 mm, drying matte to weakly glossy, dark reddish brown; berries not known. JUVENILE plants with leaf blades \pm lanceolate and weakly cordulate at base, 14.5×4 cm; anterior lobe 13.5×4 cm; posterior lobes 9×10 mm, with inner margin possibly decurrent onto petiole; primary lateral veins 4 pairs.

Phenology. Flowering in *Chlorospatha longiloba* is only known to occur during the months of July, October, and November. Inflorescences are fragrant and emerge in quick succession, with each reaching anthesis approximately one to three days after anthesis of the preceding inflorescence.

Etymology. The epithet is taken from the Latin “longus,” meaning “long,” and “lobus,” meaning “lobed,” referring to the long anterior lobe of the leaf of the new species.

Discussion. *Chlorospatha longiloba* is known only from premontane wet forest on the western slopes of the Andes, at 300–800 m elevation in Carchi and Esmeraldas provinces in northwestern Ecuador, part of the frontier region along the Colombian border. The species would be expected to occur in Pichincha to the south and northward into Nariño Department in southern Colombia.

Chlorospatha longiloba is a member of *Chlorospatha* sect. *Occidentales* and is distinguished by its green-drying, sagittate, oblong-elliptic leaf blades with relatively short, narrow posterior lobes and by its small inflorescence with a more or less purple spathe tube. *Chlorospatha longiloba* can be terrestrial or hemiepiphytic. The authors have observed the species growing on the moss-covered trunks of trees and palms, with the apex of the stem 4 m above the ground. Also unusual is the flowering habit of this species in which the petiole is sheathed approximately one half of its length, but the sympodium is subtended by a sympodial cataphyll that emerges near the base of the sheath. The species is one of only two species in *Chlorospatha* sect. *Occidentales* with a

cataphyll for the sympodial leaf, and it is also distinguished by its pink or bright orange sterile flowers (see discussion under *C. grayumii*).

The leaf blades of *Chlorospatha longiloba* are somewhat variable even within single populations, and can be either sagittate and weakly widest at the base or subsagittate, widest across the anterior lobe and cordulate at the base, with the posterior lobes much shorter and rounded at the apex.

Paratypes. ECUADOR. **Carchi:** San Marcos Valley, 600 m, $1^{\circ}07'N$, $78^{\circ}22'W$, 20–24 Nov. 1983, A. Barfod et al. 48823 (AAU, MO, QCA). **Esmeraldas:** Lita–San Lorenzo rd., 15.8 km W of new Río Lita bridge (after 1998), 800 m, $0^{\circ}53'45''N$, $78^{\circ}31'57''W$, 9 Oct. 1999, Croat, R. Mansell, L. P. Hannon & B. Owen 83174 (K, MO, US); Km. 8 on Lita–Alto Tambo rd., 749 m, 19 July 1988, C. Dodson & A. Gentry 17519 (MO, QCNE).

41. *Chlorospatha longipoda* (K. Krause) Madison, Selbyana 5(3–4): 353. 1981. Basionym: *Caladium longipodum* K. Krause, Notizbl. Bot. Gart. Berlin-Dahlem 15: 43. 1940. TYPE: Ecuador. Pastaza: Río Topo, 1200 m, 4 July 1938, A. Schultze-Rhnhof 2591 (holotype, B!). Figures 4B, 32A–D, 33A.

Chlorospatha madisonii J. Haager & J. Jeník, Preslia, Praha, 56: 165–167. 1984. TYPE: Ecuador. Napo: Río Borja, vic. San Francisco de Borja, 15 km NNE of Baeza, near Baeza–Lago Agrio rd., ca. 1200 m, $0^{\circ}25'N$, $77^{\circ}50'W$ (est.), Dec. 1981, J. Haager & J. Jeník s.n. (holotype, PR).

Terrestrial or occasionally hemiepiphytic herb, to 40 cm tall, usually in small colonies; stem fleshy, decumbent, 20–40 cm long, erect to 15 cm at apex, remnants of old cataphylls and leaf bases persisting \pm intact to semi-intact along its length; sap milky or transparent; internodes usually short, (0.5–)1–2(–4–6) cm \times 6–13 mm, matte to weakly glossy (rarely semiglossy), dark green, occasionally weakly purplish, rarely pale brownish green, drying medium greenish brown; cataphylls 6–15 cm long, inequilateral, acuminate or obtuse with acumen (rarely apiculum) at apex, acutely or obtusely 1- to 2-ribbed abaxially, pale to medium green, rarely purple-mottled in transverse bands, drying matte, medium to medium-dark reddish brown. LEAVES 3 to 5, erect to erect-spreading; **petioles** (10–)13.5–29 cm long, glabrous, matte, medium to dark green, occasionally purple-mottled in narrow transverse bands in basal 2/3, drying matte to weakly glossy, dark brown or greenish brown, sheathed 8–14 cm, 1/3 to 1/2 of total length (rarely 1/4); sheath in-rolled or erect with margins in-rolled, decurrent or free ending at apex; free portion 2–3 mm diam. midway, terete, or terete midway and subterete toward apex,



Figure 32. *Chlorospatha longipoda* (K. Krause) Madison. —A. Plant habit, showing adaxial blade surfaces. —B. Habit, showing adaxial leaf blade surfaces. —C. Leaves with abaxial blade surfaces visible at top as well as remnants of the several persistent cataphylls and leaf bases. —D. Close-up of the post-anthesis inflorescence with the spathe blade erect and cucullate. A photographed from the collection Croat *et al.* 86584 (MO). B, C photographed from the collection Croat 87303 (MO). D photographed from the collection Croat & L. P. Hannon 86644 (MO).

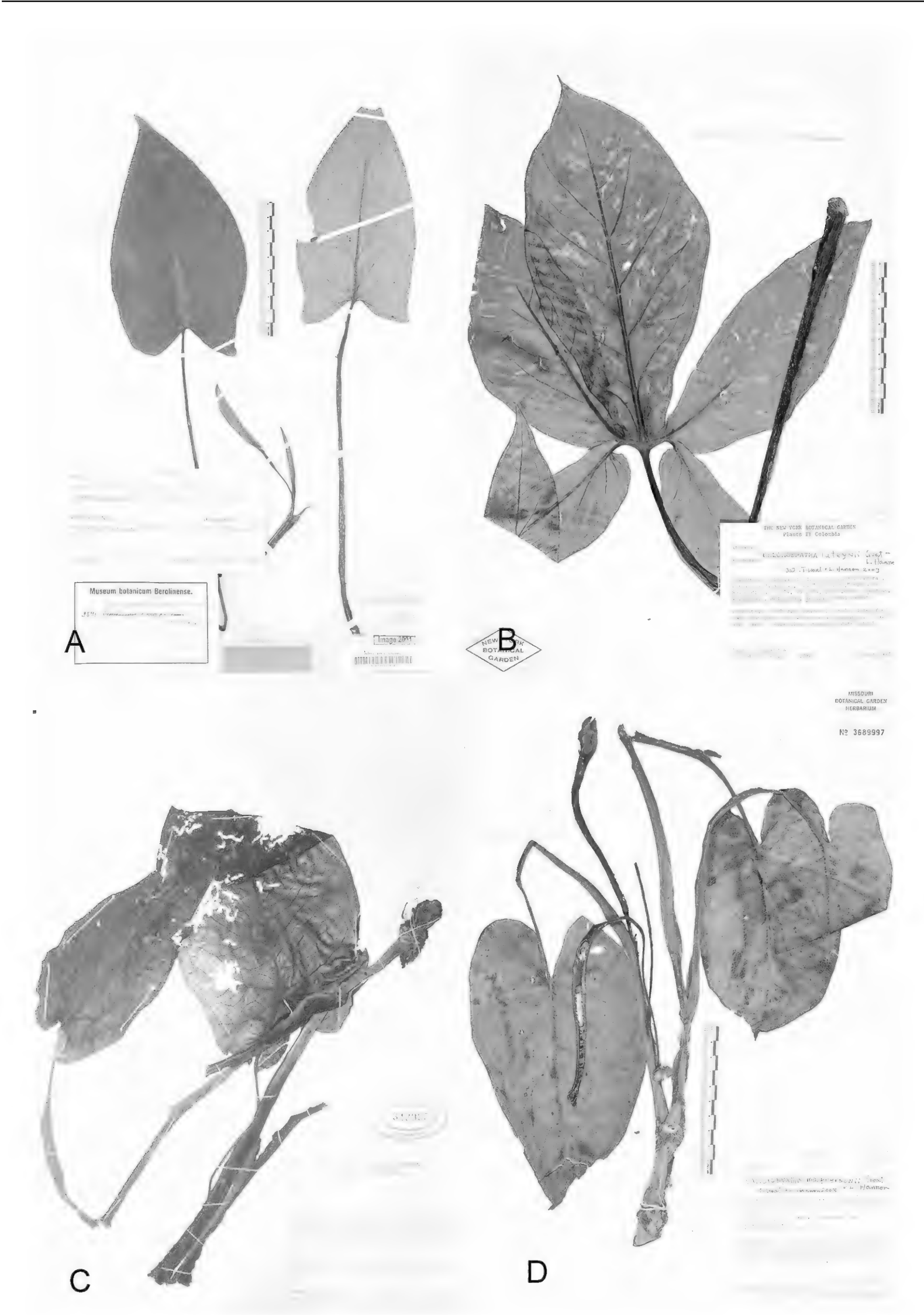


Figure 33. —A. *Chlorospatha longipoda* (K. Krause) Madison, photographed from *Schultze-Rhonhof* 2591 (from holotype at B). —B. *Chlorospatha luteynii* Croat & L. P. Hannon, *Luteyn & Callejas* 11780 (NY holotype). C, D. *Chlorospatha macphersonii* Croat & L. P. Hannon. —C. Isotype specimen, *Luteyn & O. Escobar* 12757 (COL-343995). —D. Paratype specimen, *McPherson et al.* 12903 (MO-3689997).

obscurely sulcate, bluntly V-sulcate to bluntly and narrowly sulcate or entirely sharply C-shaped and deeply narrowly sulcate, rarely sparsely and weakly granular-puberulent; **blades** narrowly ovate or ovate-elliptic, subcordate to subsagittate at base, (10–) 15.5–21.5 × (3.5–) 5–13 cm, 1.6 to 2 times longer than wide, usually broadest across anterior lobe, 1.1 to 2 times wider across anterior lobe than at base (measured tip to tip across posterior lobes), occasionally as broad as or weakly wider at base on drying, weakly or not at all constricted in area of petiole attachment, thin to thinly coriaceous, prominently bicolorous, rarely moderately so; upper surface broadly quilted, matte, matte-subvelvety, velvety or semiglossy, medium to dark green, drying matte to weakly glossy, medium to dark green or brownish to yellow-brown; lower surface reticulate, narrowly colliculate along all venation, matte, drying weakly glossy, moderately paler; anterior lobe (8.8–) 14–18 × (3.5–) 5–10(–13) cm, 1.4 to 2.3 times longer than wide, (3 to) 3.5 to 10(to 11.6) times longer than posterior lobes, weakly to moderately acuminate to bluntly acute or apiculate at apex, broadest below middle; posterior lobes directed toward the base, occasionally weakly outward, 1.5–4(–6) × 1.5–4(–5) cm, usually as long as wide, rarely 1.2 times longer than wide, broadly to occasionally narrowly rounded at apex, broadest at base, occasionally markedly inequilateral, the inner side narrower, weakly rounded to acute at base and decurrent onto petiole; outer side 5 to 6 times wider than inner side midway; midrib and major venation occasionally in part weakly granular-puberulent on lower surface, matte, concolorous or weakly to moderately darker than surface; midrib deeply sunken on upper surface, convex or moderately to narrowly round-raised on lower surface, matte, drying raised, moderately darker than surface; **basal veins** 1 to 3 pairs, coalesced into a prominent posterior rib, or with 3 to 4 branching off, 2 to 3 acroscopic, 2 to 3 basiscopic, with first and second or also the third fused, forming a short posterior rib 5–10 mm long; primary lateral veins 4 to 6 pairs, arising at 17°–45°, most acutely toward apex, ± arcuate, quilted-sunken on upper surface, convex to narrowly round-raised on lower surface, drying weakly raised, darker than surface; secondary veins in part weakly sunken on upper surface, raised on lower surface, occasionally in part sparsely granular-puberulent, darker than surface, drying raised, weakly to moderately darker than surface; tertiary veins bluntly to acutely raised or prominulous on lower surface, darker than surface, drying entirely or in part weakly darker than surface; reticulate veins weakly raised or prominulous on lower surface,

concolorous to weakly darker than surface, drying entirely prominulous or weakly raised, or in part weakly raised and otherwise prominulous, weakly darker than surface; collective veins 2 to 3(4), the innermost arising from one of the lowermost lateral veins on inner side of posterior lobe, moderately scalloped, 3–9 mm from margin. **INFLORESCENCES** erect, 1 to 6 per axil, emitting a weak fruity fragrance at anthesis; sympodium held within a sympodial cataphyll; sympodial cataphyll 6.5–8.5 × 1–2 cm, acuminate at apex, 1-ribbed abaxially, medium green, occasionally weakly purple-speckled (*Croat & L. P. Hannon 86941*); peduncle terete, 4–10 cm × 1–2 mm (to 13 cm long in fruit), weakly glossy, pale to pale-medium green, occasionally purple-tinged, drying ca. 1 mm diam., dark brown; **spathe** erect and weakly cucullate, 4–8 cm long (1–3.5 cm longer than spadix), oblanceolate, briefly acuminate or cuspidate at apex, opening narrowly most of its length at anthesis, with margins directed forward; spathe tube matte to weakly glossy, entirely pale to dark green or weakly to heavily purple-tinged on outer surface, weakly glossy to semiglossy, green on inner surface, 1–2.5 cm long, drying 3–5 mm diam., matte, dark brown; spathe blade weakly glossy, entirely pale to dark green or dark purple, or weakly to strongly purple-tinged to purple-mottled on outer surface, weakly glossy to semiglossy or matte, pale to dark green on inner surface, 2.5–6 cm long, 1.2–2 cm wide (flattened), drying matte, dark brown to purplish, occasionally moderately paler than tube, marcescent, erect after anthesis; **spadix** erect, occasionally curving forward at anthesis, (3.3–) 4.3–5.3 cm long, sessile, ± cylindrical, adnate to spathe 6–8 mm at base, ca. 1/2 of the length of pistillate portion; pistillate portion whitish, pale yellow or pale green to yellow-green, (0.7–) 1–1.8 cm × 2–3.5 mm, broadest midway; fertile staminate portion white or whitish to whitish green or pale yellow, 2–3 cm × 2–3 mm, bluntly acute at apex, ± cylindrical, drying yellow to yellow-tan; sterile staminate portion whitish (rarely violet-red), 4–8 × ca. 2 mm, weakly narrower than pistillate and fertile staminate portions; pistils weakly coherent, 2 to 3 across the axis (viewed from above), ca. 1 mm long, rarely in whorls instead of spirals (one inflorescence of *Croat et al. 86561*); ovaries whitish, cream or pale green, 1.2–2 mm diam., ± cylindrical to obtusely obconical, usually broadly depressed medially, 2- to 3-locular, with pseudoaxile placentation, the placentae fused at base, or rarely 1-locular with basal placentation and vestigial septa present (*Croat et al. 86607*); ovules 8 to 12 per locule, anatropous, biseriate or occasionally 1-seriate; funicle shorter than ovule; style Type 1

(Fig. 1), 1.2–1.3 mm diam., as broad as ovary apex, occasionally obscurely attenuate medially, the margin obscure or distinct, not coherent with those of adjacent styles; red chromoplasts present; **stigma** white to cream, sessile, occasionally obscurely elevated on style, 0.2–0.3 mm diam., obpyramidal or cylindrical; synandria ca. 1 mm long, $1.3\text{--}1.5 \times 1.1\text{--}1.2$ mm diam. and \pm elongated in direction of axis, occasionally highly bilaterally symmetrical, coherent, weakly or prominently deeply (2)3- to 4(5)-lobed (occasionally almost to center), broadly concave medially, with lobes thickened, occasionally subrounded, the margins sinuate-undulate and interlocking with those of adjacent flowers, (2)3- to 4(5)-androus, the thecae each with a terminal pore; sterile flowers occasionally purple-tinged in basal 2 whorls, rarely violet-red, less than 1 mm long, $1.3\text{--}2 \times 1\text{--}1.3$ mm diam. and \pm elongated in direction of axis, coherent, truncate, subprismatic to irregularly prismatic, in 3 to 5 whorls. **INFRUDESCENCE** pendent, entirely green or occasionally purple-tinged, (2.5–)3–4 cm \times (6–)7–10 mm, drying matte to weakly glossy, dark brown; berries cream-colored or pale green and weakly violet-tinged apically, 4–5 mm diam., drying yellowish brown; seeds 7 to 8 per berry, $1.2\text{--}2 \times 0.8\text{--}1$ mm, obtusely 3-sided, rounded at base, acute at apex, finely costate, drying cream-colored.

Phenology. Flowering is known to occur in *Chlorospatha longipoda* during the months of January, April, May, July, August, September, and December, and probably occurs throughout the year. Inflorescences are fragrant and emerge in quick succession, each reaching anthesis approximately one to three days after anthesis of the preceding inflorescence. Fruiting is recorded for the months of April, August, and November.

Discussion. *Chlorospatha longipoda* is widespread on the eastern slopes of the Andes in Ecuador, at (265–)470–1700 m elevation, occurring in Morona-Santiago, Napo, Pastaza, Sucumbíos, Tungurahua, and Zamora-Chinchipe provinces. The species probably occurs also in Chimborazo Province. As is true of other wide-ranging species from the eastern slopes, *C. longipoda* occurs in a wide variety of life zones: tropical wet forest, premontane wet forest, lower montane wet forest, premontane rainforest, premontane moist forest, and montane moist forest. Although the notation of the localities is imprecise, it appears that *C. longipoda* occurs on the eastern slopes of the Cordillera de Cutucú in Morona-Santiago and, therefore, is likely to occur also in Peru. The species is found in deep shade, frequently

in small colonies, and can be common and widespread in the dark understory in some areas, such as the collection sites of *Croat & L. P. Hannon* 87003, off of the Macas–Puyo road, on the road to Palora, and *Croat & L. P. Hannon* 86607, near the town of Shell, on the Puyo–Baños road. In the original publication of the type, “Río Topo” is possibly a misprint. No record of this river could be located. However, there is a Río Toro at approximately the same GPS coordinates as those for Hacienda Topo and the town of Topo, at this elevation.

Chlorospatha longipoda, the type species for *Chlorospatha* sect. *Orientalis*, is distinguished by its usually narrowly ovate-elliptic leaf blades that are subcordate to subsagittate at the base, with the posterior lobes short and usually rounded at the apex, and the inner margins decurrent onto the petiole. The upper surface is broadly quilted, frequently velvety, and the lower surface is matte and conspicuously reticulate. The species is also characterized by the presence of a sympodial cataphyll, its matte, medium to dark green petiole, sheathed one third to one half of its length, short peduncle (4–10 cm long) and small inflorescence, 4–8 cm long, with the spadix adnate to the spathe ca. one half of the length of the pistillate portion. The spathe can be entirely green or the tube can be weakly to moderately purple-tinged, or the blade can be partially purple-tinged to entirely dark purple and the tube green. *Chlorospatha longipoda* has been observed as a hemiepiphyte growing low on the bases of trees, a habit observed in no other species from the eastern slopes, although it is likely that it occurs in other species.

Chlorospatha longipoda exhibits considerable variation in the texture of the upper surface of the leaf blade, ranging from velvety to semiglossy, and some variation in blade shape, some blades having extremely short posterior lobes (less than 2 cm long), others having longer lobes with more well-developed posterior ribs. *Croat* 59100 differs in having a more broadly sagittate blade that dries yellow-brown, with longer posterior lobes and the abaxial venation more conspicuously raised than is typical. *Croat & L. P. Hannon* 86607 has leaf blades both narrowly triangular and narrowly ovate-elliptic on single plants, with some posterior lobes directed slightly outward and narrowly rounded at the apex. Considering the amount of variation in *C. longipoda* and the fact that many of the collections cited here are sterile, it is possible that more than one taxon or species is represented; however, the variation in blade shape occurs within single populations as well as between different populations, though the variation in the texture of the upper blade surface apparently occurs

only in different populations. The distinguishing characters of the species are otherwise consistent. Small, juvenile plants of several species from the eastern slopes are nearly identical to juvenile or even in some cases, adult plants of *C. longipoda*: *C. boosii*, *C. engleri*, *C. hannoniae*, *C. limonensis*, *C. plowmanii*, and *C. pubescens*. In these six species, the shape of the juvenile blade is similar to that of the juvenile and mature blades of *C. longipoda*. This, combined with a consideration of the variability of blade shape in most species in section *Orientales*, would suggest a close relationship between these species. In the past, there has been some confusion regarding determinations of *C. longipoda*, and, because of this, its in-depth discussion seems appropriate.

Madison (1981) combined *Caladium plowmanii* (Madison, 1976) with *Chlorospatha longipoda* without examining the type of *C. longipoda*. *Caladium plowmanii* differs from *C. longipoda* in significant ways and is better combined in a new species, *Chlorospatha plowmanii* (Madison) Croat & L. P. Hannon. *Chlorospatha plowmanii* is also widespread on the eastern slopes of the Andes in Ecuador. To date, the two species have not been observed together, but are probably sympatric in Morona-Santiago and Napo provinces. The remnants of old cataphylls and leaf bases persist more or less intact along the stem of *C. longipoda*, but only as semi-intact fragments or short fibers in *C. plowmanii*. Throughout its range, *C. longipoda* has narrowly oblong-elliptic leaf blades, subcordate or subsagittate at the base, with the posterior lobes short, broad, and usually rounded at the apex and the anterior lobe (3.1 to) 3.5 to 10 times longer than the posterior lobes. The blades of *C. plowmanii* are subhastate to hastate, conspicuously broadest at the base, frequently as wide as long, with the posterior lobes long, narrow, and usually acute at the apex (rarely narrowly rounded), and the anterior lobe only 1.5 to 2 times longer than the posterior lobes. The posterior rib is naked 3–5(–10) mm on each side in *C. plowmanii*, but not naked in *C. longipoda*. There are four to six pairs of primary lateral veins in the latter species and three or four pairs in *C. plowmanii*. The spathe of *C. longipoda* is weakly to moderately cucullate, with the blade erect after anthesis. In *C. plowmanii* the blade is erect to erect-spreading at anthesis, but reflexes after anthesis and is quickly deciduous, a presumably unique condition in *Chlorospatha*. The ovaries of the latter species are 1- or 2-locular versus 2- or 3-locular in *C. longipoda*. The synandria of *C. plowmanii* are 2- or 3(4)-androus, differing from those of *C. longipoda*, which are (2)3- or 4(5)-

androus. The inflorescence of the latter species is fragrant, whereas that of *C. plowmanii* is odorless.

Chlorospatha longipoda could possibly be confused with two species from Morona-Santiago Province, both of which occur in the Limón–Méndez region, at about 900 m elevation, *C. boosii* and *C. hannoniae*, and are probably sympatric with *C. longipoda* (see discussions under *C. boosii* and *C. longipoda*).

Krause (1940: 43) described the lower surface of the leaf blade of the type (*Schultze-Rhonhof* 2591) as having “sparse, short, prominent, white hairs.” When the authors examined the type, no hairs were observed on the blade surface, but some sparse, random granular-puberulence was observed on the secondary venation, occasionally on the midrib, major, and secondary venation of other collections.

Chlorospatha madisonii J. Haager & J. Jeník was deemed to be the same species as *C. longipoda*.

Additional specimens examined. ECUADOR. **Morona-Santiago:** Laguna Sardina & Volcán al Upano, Parque Nac. Sangay, 1750 m, *C. Cerón et al.* 48784 (QAP); vic. Río Furubumbo, Parque Nac. Sangay, 1450 m, *C. Cerón et al.* 48890 (QAP); Macas–Riobamba, 17.3 km N of Macas, 1015 m, *Croat et al.* 86561 (AAU, B, CAS, COL, F, GH, HUA, INB, K, M, MEXU, MO, MY, QCA, QCNE, RSA, S, SEL, UB, US, VEN); vic. Humboya, 10.5 km W of Puyo–Macas rd. (Hwy. 45), 6.6 km N of Río Chiguaza, *Croat & L. P. Hannon* 86917 (CM, CUVC, JBGp, MO, QCNE, U); along Palora–Río Amundalo rd., 5.3 km NW of Palora, at Río Amundalo, 0.3 km N of San Vicente at Tarquí, 932 m, *Croat & L. P. Hannon* 86941 (MO, QCNE); Puyo–Macas rd. to Palora, 9.8 km from main rd., *Croat & L. P. Hannon* 87003 (KRAM, L, MO, QCNE); along Gualaquiza–Indanza rd., 12 km S of Indanza, along river, 1336 m, *Croat* 87303 (K, MO, QCNE, US); Cord. de Cutucú, ca. 25 km SE of Logroño on footpath to Yaupi, 900 m, *Madison & Coleman* 2520 (SEL), 800 m, *Madison & Coleman* 2567 (QCA, SEL); along Logroño–Yaupi trail, 1500 m, *Madison et al.* 3357 (QCA, SEL, US); 20 km S of San Juan Bosco, 1300 m, *Madison & Besse* 7557 (SEL). **Napo:** along rd. betw. Baeza & Tena, 37.7 km S of Baeza, 59 km N of Archidona, 1700 m, *Croat* 58780 (MO); Archidona–Baeza, vic. Jondachi, 20.1 km N of Baeza, 5 km S of turn-off to Loreto, 1033 m, *Croat et al.* 87777 (MO); Río Borja, vic. San Francisco de Borja, 15 km NNE of Baeza, near Baeza–Lago Agrio rd., 1981, 1200 m, *Haager & Jeník s.n.* (PR); Res. Prod. Faun. Cuyabeno, N of Laguna Grande, 1265 m, *A. D. Poulsen* 80065 (AAU, MO). **Pastaza:** Mera, forest near Mangayacu, 1100 m, *E. Asplund* 19095 (S); along Puyo–Baños rd., second bridge W of Mera, ca. 3 km W of Mera, 1165 m, *Croat* 49715 (MO); along Puyo–Macas rd., Km. 19 (S of Puyo), 1200 m, *Croat* 50570 (MO); along rd. betw. Puyo & Diez de Agosto & Arajuno, 18 km NE of main Puyo–Macas rd. (beginning 3.7 km from center of Puyo, at Hotel Europa), 8.2 km NE of Diez de Agosto, 970 m, *Croat* 59062 (MO, QCNE); along Puyo–Baños rd., 11.9 km W of Shell, 3.9 km W of Mera, 1100 m, *Croat* 59100 (CM, MO, QCA, QCNE); Macas–Puyo, 1.2 km S of Yantana, 38.4 km S of Veracruz, 951 m, *Croat et al.* 86584 (K, MO, QCNE); vic. Shell, to N, off of main Puyo–Baños rd., 1096 m, *Croat & L. P. Hannon*

86607 (AAU, B, CAS, F, MEXU, MO, NY, QCNE, SEL, US); vic. Shell, along rd. N to Río Alpayacu 0.8 km, 1121 m, *Croat & L. P. Hannon 88917* (CM, CUVC, JBCP, MO, QCNE, U); along Puyo–Macas rd., 3 km SE of Veracruz, 900 m, *G. Harling & L. Anderson 16816* (MO). **Sucumbíos:** along Lumbaquí–La Bonita rd., departing main Baeza–Lago Agrio rd. just E of Río Aguarico bridge E of Lumbaquí, 5.8 km NW of jct. with main hwy., 400 m, *Croat et al. 93580* (MO, QCNE). **Tungurahua:** Río Negro to Parque Nac. Sangay, 4.9 km S of Río Negro, on rd. departing main Puyo–Baños rd., 1520 m, *Croat & L. P. Hannon 86644* (AAU, GB, K, MO, NY, QCNE, S, SEL, US); 1.8 km S of Río Negro, on rd. departing main Puyo–Baños rd., 1338 m, *Croat & L. P. Hannon 86662* (BR, GB, INB, M, MO, GH, P, QCNE, RSA, U, UB, USM, WU); along rd. from Río Negro to La Estancia & Parque Nac. Sangay, 1.8 km S of bridge over Río Pastaza, 1335 m, *Croat & L. P. Hannon 88495* (ENCB, MO, QCNE); *88514* (GB, MO, QCNE, TEX, WU). **Zamora-Chinchipe:** Paquisha S to Las Orquídeas, at end of Río Nangaritza rd. via Guayzimi, beginning at 15.9 km E of Zumbi & Río Nangaritza, then 46 km S of intersection near Paquisha, 875 m, *Croat et al. 91356* (MO, QCNE).

42. *Chlorospatha luteynii* Croat & L. P. Hannon, *Aroideana* 27: 24. 2004. TYPE: Colombia. Antioquia: Mpio. Carmen del Viboral, vic. La Milagrosa, vía “El Canada,” Finca La Soledad, 2400–2600 m, ca. 6°05'N, 75°25'W, 27 Oct. 1987, *J. Luteyn & R. Callejas 11780* (holotype, NY!; isotypes, HUA!, NY!). Figures 28D, 33B.

Terrestrial herb, to 1 m tall; stem not known; internodes not known (all measurements made from dried material); cataphylls not known. LEAVES 2 to 3, erect-spreading; **petioles** 40–90 cm long, glabrous, drying glossy, dark blackish brown, with epidermis in part separated \pm intact and semi-transparent, sheathed 20–55 cm, 1/2 or slightly more of total length; sheath decurrent at apex; free portion 4–6 mm diam. midway; **blades** deeply 5-lobed, occasionally weakly auriculate on outermost segments, ca. 35 \times ca. 31–40 cm, almost as wide as long, drying thin, weakly bicolorous; upper surface dark green, irregularly pale yellow-green maculate (maculations 7–30 \times 3–12 mm), drying weakly glossy to semiglossy (matte), dark green to olive-green, maculations paler; lower surface drying semiglossy to glossy, maculations weakly paler or not visible; **medial lobe** 24–31 \times 12–16 cm, 1.8 to 2.5 times longer than wide, abruptly acuminate at apex, broadest at or slightly above middle, cuneate toward and narrowly attached at base, 3–4 cm wide at point of attachment, \pm symmetrical; **lateral lobes** confluent with all adjacent lobes, the confluent portion 1.5–4 cm wide; innermost segment 20–27 \times 8–10.5 cm, 2.3 to 2.8 times longer than wide, acuminate at apex (rarely acute), broadest at or above middle, narrowly attached at base, 3–3.5 cm wide at point of attachment, moderately inequilateral, the inner side narrower, \pm

straight to weakly convex toward base, occasionally weakly attenuate; outer side to 1.9 times wider than inner side midway, weakly convex toward base; outermost segment 15–18.5 \times 5–7 cm, 2.6 to 3 times longer than wide, acuminate at apex, broadest midway, narrowly to broadly attached at base, 2–3.5 cm wide at point of attachment, moderately inequilateral, the inner side narrower, \pm straight toward base; outer side 1.3 to 1.5 times wider than inner side midway, weakly to broadly rounded toward the base or forming an auricle 5.5 \times 2 cm; midrib and major venation round-raised on lower surface, drying much darker than both surfaces, almost black, \pm flattened on lower surface; posterior rib naked 2–3.5 cm per side; primary lateral veins (on medial lobe) 5 to 6 pairs, arising at 25°–40°, \pm straight; primary lateral veins (on lateral lobes) 4 to 5 pairs, arising at 25°–35°, weakly arcuate; secondary veins drying in part raised on lower surface, otherwise prominulous, occasionally flattened, moderately darker than surface; tertiary and reticulate veins drying in part prominulous on lower surface, otherwise visibly distinct, usually moderately darker than surface; collective veins 3, the innermost arising from lowermost lateral vein at base, loop-connected with all preceding lateral veins, moderately scalloped, 0.4–1.2 cm from margin. INFLORESCENCES erect, to 3 per axil; peduncle held within the sheath, 20–43 cm \times ca. 2 mm, drying weakly glossy, dark blackish brown; **spathe** pale green, erect, 9–12 cm long; spathe tube 4.3–5 cm \times 5–6 mm, drying matte, dark brown on outer surface, weakly glossy, paler and densely tan, punctiform on inner surface (speckles regularly rounded, appearing as subepidermal cellular inclusions); spathe blade 5.5–7 cm \times 7–8 mm, acuminate at apex, drying matte, dark reddish brown (paler than tube), marcescent, erect after anthesis; **spadix** erect, weakly stipitate 1–2 mm (stipe emerging from a small sheath in spathe), 8.5–9.5 cm long, adnate to spathe 2.7–3.6 cm at base, most of the length of pistillate portion; pistillate portion 2.9–3.7 cm \times ca. 4 mm, broadest midway, drying brownish; fertile staminate portion white, 5–6 cm \times ca. 3–6 mm, bluntly acute at apex, narrowed at base, tapering, drying medium-dark brown to reddish brown; sterile staminate portion 1.4–1.6 cm \times 1.5–2.2 mm, narrowest midway, drying dark tan; pistils weakly coherent, ca. 4 to 5 across the axis (viewed from above), ca. 1.2 mm long; ovaries subglobose, 1.5–2 mm diam., drying cream to tan; style Type 3 (Fig. 1), 1–2 mm diam., weakly broader than ovary apex, the margins not coherent with those of adjacent styles; **stigma** 0.3–0.5 mm diam., sessile; synandria ca. 1–1.5 \times 1–2 mm, coherent, truncate, deeply (2)3-

to 4-lobed, (2)3- to 4-androus (either mostly 3- or mostly 4-androus on different specimens); sterile flowers ca. 1 mm long, $1.8\text{--}3 \times 1$ mm diam. and \pm elongated in direction of axis, coherent, truncate, subprismatic, in 6 to 7 whorls. Berries not known.

Phenology. Flowering is only known to occur in *Chlorospatha luteynii* during the months of April and October, with fruiting reported for October.

Discussion. *Chlorospatha luteynii* is known only from lower montane wet forest in the northern portion of the Cordillera Central in Antioquia Department, Colombia, at 2440–2800 m elevation and would be expected to occur elsewhere in the department on both sides of the Cordillera Central, possibly to the south into Caldas and on the eastern slopes of the Cordillera Occidental in Risaralda. *Chlorospatha luteynii* is a member of *Chlorospatha* sect. *Chlorospatha* and is distinguished by its deeply 5-lobed, dark green, conspicuously pale yellow-green maculate leaf blades that dry dark green to olive-green on both surfaces and more or less glossy on the lower surface, with the midrib and major venation almost black on both surfaces. The species is also distinguished by its petiole, which dries semiglossy, almost black, with the epidermis partially separated intact, and by its entirely pale green spathe. The spadix is noteworthy in having the fertile staminate portion much longer than the pistillate portion, almost twice as long. In *Chlorospatha*, the fertile staminate portion is usually shorter, weakly longer than or equal in length to the pistillate portion. The sterile staminate portion is also relatively long (1.4–1.6 cm) and densely flowered, with the sterile flowers markedly elongated in the direction of the axis to 3 mm long (as viewed from above).

Chlorospatha luteynii could be confused with *C. caldasensis*, which occurs to the south on the western slopes of the Cordillera Central in Caldas Department at similar elevations. Grayum (1986) predicted that *C. croatiana* subsp. *croatiana*, known only from Central America at 200–1173(–1400) m elevation, would ultimately be found in Colombia, and although that species and *C. luteynii* have 5-lobed leaf blades in common, *C. luteynii* should be considered distinct (see discussions under *C. caldasensis* and *C. croatiana* subsp. *croatiana*).

Additional specimens examined. COLOMBIA. **Antioquia:** Mpio. Sonsón, vía Sonsón–La Soledad, 1.1 km E of the branch in rd. leading N to La Morelia, vic. Manzanares, 2800 m, 8 Apr. 1988, *Callejas 6361* (HUA); Mpio. Caldas, vic. La Corrala, Finca La Zarza, 2440 m, 1 June 1988, *L. Escobar et al. 8482* (HUA).

43. *Chlorospatha macphersonii* Croat & L. P. Hannon, *Aroideana* 27: 27. 2004. TYPE: Colombia. Antioquia: Mpio Jardín, vic. Ventanas, Jardín–Ventanas–Riosucio rd., ca. 19.3 km SSE of Jardín, at border with Caldas, forest at high point of rd. (Ventanas), 2830 m, $5^{\circ}40'N$, $75^{\circ}47'W$, 4 May 1989, *J. Luteyn & O. Escobar 12757* (holotype, NY!; isotypes, COL-343995!, HUA!). Figures 33C, D, 36C.

Terrestrial herb, 50–60 cm tall (all measurements made from dried material); stem occasionally weakly woody, decumbent, with remnants of old cataphylls persisting semi-intact at upper nodes; internodes $2\text{--}6 \times 0.6\text{--}2$ cm, drying finely wrinkled, matte to weakly glossy, pale-medium brown, occasionally weakly gray-tinged; cataphylls 12–18 cm long, acuminate at apex, drying matte to weakly glossy, medium reddish brown. LEAVES 3, erect-spreading; **petioles** 25–34 cm long, drying glabrous, matte, dark brown, frequently blackish toward apex, sheathed 21–26.5 cm, slightly more than $3/4$ of total length; sheath free-ending at apex; free portion 2.5–4 mm diam. midway, sulcate; **blades** ovate-cordate, $17\text{--}25 \times 9\text{--}12.5$ cm, 1.7 to 2 times longer than wide, gradually or abruptly acuminate at apex, broadest at or slightly below middle, weakly broader across anterior lobe than at base (measured tip to tip across posterior lobes), rarely much broader, fleshy; upper surface weakly bullate, drying matte to weakly glossy, dark yellow-brown; lower surface reticulate, drying semiglossy, yellow-brown to yellow-green, weakly to moderately paler; anterior lobe $13\text{--}19 \times 9\text{--}12.5$ cm, 1.3 to 1.6 times longer than wide, (2.8 to)3.8 to 4.8 times longer than posterior lobes, broadest at or below middle, \pm symmetrical to weakly inequilateral; posterior lobes directed toward the base, $3\text{--}5 \times 3.5\text{--}5$ cm, usually as wide as long, occasionally wider than long, bluntly to narrowly rounded at apex, broadest at base, the sinus oblong to narrowly V-shaped or closed with the lobes overlapping; sides \pm symmetrical, the inner side acute to weakly rounded toward base, briefly attenuate and weakly confluent with opposite lobe, obscuring petiole apex; outer side weakly convex; all orders of venation \pm sunken on upper surface, moderately to prominently raised, \pm granular-puberulent on lower surface, drying \pm raised, concolorous or weakly paler to weakly darker than surface, frequently tan-colored; midrib round-raised on lower surface; **basal veins** 4 to 5 branching off, 3 to 4 acroscopic, 1 to 2 basiscopic, the first usually free to the base, second and/or third fused, forming a short posterior rib 0.5–2 cm long; primary lateral veins 4 to 5 pairs, arising at $40^{\circ}\text{--}60^{\circ}$, weakly arcuate; collective veins 3, the innermost arising from one of

the lowermost basal veins, loop-connected with all preceding lateral veins, moderately scalloped, 3–11 mm from margin. INFLORESCENCES erect, 2 to 3 per axil; peduncle held within the sheath, 17–20 cm \times 1–3 mm, drying matte, dark blackish brown; **spathe** erect, ca. 15 cm long, acuminate at apex; spathe tube green or greenish red on outer surface, 8–8.5 cm \times 6–7 mm, drying matte, dark blackish brown on outer surface, weakly glossy and red-tinged on inner surface; spathe blade whitish green to yellowish green on outer surface, ca. 6.3 cm \times 7–7.5 mm, drying weakly glossy, dark blackish brown on outer surface, weakly glossier on inner surface; **spadix** erect, ca. 12.2 cm long, sessile, adnate to spathe ca. 7.5 cm at base, the entire length of pistillate portion and onto sterile staminate portion ca. 7 mm; pistillate portion ca. 6.7 cm \times ca. 4 mm, weakly broadest midway; fertile staminate portion white, ca. 4.7 cm \times 3–4.5 mm, narrowly rounded at apex, clavate, drying medium-dark orangish brown; sterile staminate portion ca. 1.5 cm \times 2–3 mm, broadest at apex, with axis naked in basal 3 mm, drying medium-dark orangish brown; pistils \pm laxly arranged, ca. 3 across the axis (viewed from above), ca. 2 mm long; ovaries subglobose to \pm cylindrical, ca. 1–1.5 \times 1.5–2 mm, drying dark reddish brown; style Type 10 (Fig. 1), ca. 0.5 \times 1.5–1.8 mm, comprising 1/4 to 1/3 of the length of pistil, the margins not coherent with those of adjacent styles; **stigma** ca. 0.5 mm diam., weakly elevated on and weakly broader than narrowed portion of style; synandria 1–1.5 \times ca. 2 mm, coherent, truncate, (2)3- to 4-lobed, (2)3- to 4-androus (mostly 4); sterile flowers 1–1.5 \times 1.5–2 mm, weakly coherent, in 6 whorls, 2- to 5-branched, the branches truncate and broadest at apex, weakly narrower below. INFRUDESCENCES 11–12.5 \times ca. 1 cm, drying matte, dark reddish brown (almost black) on outer surface; berries ca. 5 \times 5 mm, drying dark reddish brown.

Phenology. Flowering is only known to occur in *Chlorospatha macphersonii* during the months of May and October, with fruiting reported in October.

Discussion. *Chlorospatha macphersonii* is known only from the eastern slopes of the Cordillera Occidental, in the vicinity of Jardín, at the southern end of Antioquia Department, Colombia, near the borders with Caldas and Risaralda departments, at almost 3000 m elevation. The species occurs in premontane wet forest and premontane moist forest, possibly also in lower montane wet forest, and would be expected to occur elsewhere in Antioquia and in the adjoining departments to the south, possibly also on the western slopes.

Chlorospatha macphersonii is a member of *Chlorospatha* sect. *Occidentales* and is distinguished by its long internodes (2–6 cm long), long-sheathed petiole (more than three fourths of its length), with the sheath free-ending at the apex and ovate-cordate leaf blades that are weakly bullate on the upper surface and reticulate on the lower surface. Also noteworthy is the extraordinarily large inflorescence (ca. 15 cm long), although the plant is relatively small (50 cm tall). The inflorescences are half as long to nearly as long as the peduncles and some petioles. The species is also distinguished by its green to greenish red spathe tube and whitish to yellowish green spathe blade. The spadix is adnate to the spathe the entire length of the pistillate portion and half of the length of the sterile staminate portion, with briefly attenuated styles and 2- to 5-branched sterile flowers.

Chlorospatha macphersonii could possibly be confused with *C. munchiquensis* from the Parque Nacional Munchique on the western slopes in Cauca Department, at 2580 m elevation. Both species have long internodes, more or less bullate leaf blades, and large inflorescences. The petiole of *C. munchiquensis* is sheathed only one third of its length and the peduncle is short (13–15 cm long), thus differing from *C. macphersonii* in which the petiole is sheathed more than three fourths of its length and the peduncle is 17–20 cm long. The leaf blades of *C. munchiquensis* are ovate-sagittate, broadest at the base and dry dark brown, with the posterior lobes long, relative to the length of the anterior lobe (1.4 to 1.6 times longer than the posterior lobes), and six to eight pairs of primary lateral veins. The posterior lobes have straight, well-developed posterior ribs, with the inner margins decurrent onto the petiole (in mature plants). *Chlorospatha macphersonii* differs in having ovate-cordate blades that are broadest across the anterior lobe and dry yellow-brown, with short posterior lobes, the anterior lobe being 3.8 to 4.8 times longer, and four to five pairs of primary lateral veins. The posterior lobe has only a weak posterior rib and the inner margin is weakly confluent with the opposite lobe, thus obscuring the petiole apex. The lower surface of the blade dries semiglossy, with all orders of venation more or less raised, creating a distinct reticulate pattern. In *C. munchiquensis*, the lower surface dries weakly glossy and the reticulate venation is not prominent, thus the reticulate pattern is lacking. The inflorescence of *C. munchiquensis* is probably significantly smaller than that of *C. macphersonii*, the spathe tube of the flowering inflorescence of the latter species being 8–8.5 cm long, compared to the fully mature infructescence (spathe tube) of *C. munchiquensis*, which is only 6–8

cm long. The fruiting tube is typically twice the length of the pistillate portion of the flowering spadix in *C. macphersonii*. The spathe tube of the latter species is green and dark purple-tinged on the outer surface and entirely dark purple on the inner surface, whereas that of *C. macphersonii* is green or greenish red on the outer surface and the sterile staminate portion of the spadix is 1.5 cm long, with the sterile flowers 2- to 5-branched. The sterile staminate spadix of *C. munchiquensis* is half as long, with the sterile flowers subprismatic.

Additional specimen examined. COLOMBIA. **Antioquia:** Mpio. Jardín, S of Jardín, 2750 m, *McPherson et al.* 12903 (HUA-58996, MO-3689997, see Figs. 36C and 33D, respectively).

44. *Chlorospatha maculata* Croat & L. P. Hannon, sp. nov. TYPE: Colombia. Chocó: along rd. betw. Pueblo Rico (Risaralda) & Istmina (Chocó), along Quebrada Antón, 15 km W of Santa Cecilia, 6 km W of Chocó-Risaralda border, ca. 20 km E of Playa del Oro, 240 m, 5°20'30"N, 76°13'45"W, 22 Feb. 1990, *Croat 70901* (holotype, MO-3780535!; isotypes, K!, US!). Figure 34A, B.

Herba usque ad ca. 1 m; internodia ca. 1.5 × 1–4 cm. Petiolus 35–90 cm long, vaginatus per (12–)23–43 cm; lamina foliaris profunde 3-loba, fere trisecta, 30–48 × 27–60 cm, lobo medio 25.5–40 × 11–19 cm, nervis primariis lateralibus utroque 7 ad 10 (in lobis lateralibus). Inflorescentiae 3 in quaque axilla; pedunculus usque ad ca. 43 cm × 1 mm; spathae tubo 4.2–4.5 cm × ca. 5 mm.

Terrestrial herb, to ca. 1 m tall; stem erect, remnants of old cataphylls persisting semi-intact and ± fibrous at upper nodes; internodes ca. 1.5 × 1–4 cm, brown, scurfy (with old petiole bases), drying matte, dark brown (all measurements made from dried material); cataphylls (total length and apex not known) drying weakly glossy, medium-dark reddish brown, weakly fibrous. LEAVES 2 to 3, erect-spreading; **petioles** 35–90 cm long, brittle, glabrous, semiglossy, dark green, drying weakly glossy to semiglossy, dark reddish brown to almost black, rarely medium to dark greenish brown, sheathed (12–)23–43 cm, 1/2 to 2/3 of total length; sheath weakly free-ending at apex; free portion 4–6 mm diam. midway, terete, subterete, or convex on both surfaces with obtusely angular lateral margins toward apex; **blades** held spreading to erect-spreading, deeply 3-lobed, nearly trisect, 30–48 × 27–60 cm, 1.1 to 1.2 times wider than long, coriaceous, occasionally thinly coriaceous, moderately bicolorous; upper surface (of all lobes) broadly concave, matte, dark green, sparsely to moderately pale yellow-green maculate (macula-

tions small), drying matte to weakly glossy, dark brown, rarely pale olive-green, the maculations obscure; lower surface weakly glossy to semiglossy, drying weakly glossy to semiglossy, weakly to moderately paler, occasionally weakly gray-tinged; **medial lobe** 25.5–40 × 11–19 cm, 1.7 to 2.1(to 2.6) times longer than wide, 1.1 to 1.3 times longer than lateral lobes, gradually or abruptly acuminate at apex, broadest midway, briefly attenuate (rarely long-attenuate) to cuneate toward base and narrowly attached, 1.5–2 cm wide at point of attachment, weakly inequilateral; **lateral lobes** oblique or directed weakly toward the apex, 22–33 × 7.3–12.5 cm, usually 2.5 to 3 times longer than wide, acuminate to occasionally acute at apex, broadest below middle, markedly inequilateral, the inner side always narrower, attenuate at base and confluent with medial lobe, the confluent portion 1–3 mm wide; outer side 4 to 7 times wider than inner side midway, weakly to broadly rounded toward base, rarely narrowly rounded, frequently overlapping opposite lobe, abruptly attenuate onto posterior rib; midrib and major venation narrowly sunken on upper surface, paler than surface, drying concolorous to weakly paler than surface, round-raised on lower surface, drying ± flattened, moderately to conspicuously darker than surface; posterior rib naked 1–2 cm per side, convex on lower surface; primary lateral veins (of medial lobe) 6 to 8 pairs, arising at 35°–48°, most acutely toward apex, straight to weakly arcuate, convex on lower surface; primary lateral veins (of lateral lobes) 7 to 10 pairs (lowermost 1 to 2 pairs occasionally fused at base), with most aggregated in basal 1/3, arising at 35°–90°(–110°), most acutely toward apex, weakly to moderately arcuate; secondary veins in part narrowly sunken on upper surface, drying entirely or in part weakly raised or prominulous on lower surface, otherwise flattened, weakly darker than surface; tertiary veins usually flat on lower surface, occasionally weakly raised, darker than surface, drying ± obscure, occasionally in part weakly prominulous; reticulate veins obscure; collective veins 3, the innermost arising from one of the lowermost lateral veins at base, loop-connected with all preceding lateral veins, moderately scalloped, 3–13 mm from margin. INFLORESCENCES erect, to 3 per axil; peduncle held within the sheath, to ca. 43 cm × 1 mm, drying weakly glossy, blackish brown; **spathe** total length and apex not known; spathe tube yellow-green to greenish yellow, 4.2–4.5 cm × ca. 5 mm; spathe blade not known; **spadix** in part known; fertile staminate portion white. INFRUCTESCENCES medium green, 6–10 × 1–1.5 cm; berries ca. 5 across



Figure 34. *Chlorospatha maculata* Croat & L. P. Hannon, photos of the holotype Croat 70901 (MO). —A. Fertile habit. Note inflorescence in foreground. —B. Leaf blade adaxial surface.

the axis (viewed from above), drying creamy white, 2–5 mm diam.; seeds drying pale tan.

Phenology. The only available fertile material of *Chlorospatha maculata* was a fruiting spadix collected in February.

Etymology. The epithet is taken from the Latin “maculatus,” meaning “spotted” or “blotched,” referring to the spotted blade of *Chlorospatha maculata*.

Discussion. *Chlorospatha maculata* is known only from Chocó Department, Colombia, at 240–825 m elevation, in tropical rainforest, premontane rainforest, premontane wet forest, and lower montane wet forest on the western slopes of the Cordillera Occidental. Entirely green leaves, brittle petioles, and subcoriaceous, 3-lobed blades that are matte, maculate, and not at all quilted on the upper surface distinguish the species, a member of *Chlorospatha* sect. *Chlorospatha*. All segments are broadly concave on the upper sides (observed in photographs), a condition not previously observed in the genus, possibly resulting from the considerable thickness of the blade. It is possible that the label notes are

incorrect in this regard and that the blade is coriaceous rather than subcoriaceous. The apex of all lobes is directed above the horizontal plane, relative to the base, and the major venation is paler than the upper surface and only narrowly sunken.

Chlorospatha maculata would be most easily confused with *C. mirabilis*, which differs in having the petiole spongy and purple, the blades more or less purple on the lower surface and somewhat glossy on the upper surface, and the segments convex and quilted. The leaves of *C. maculata* are either entirely green or maculate, with the petiole brittle, the blades matte on the upper surface, not at all quilted, and the segments broadly concave. The lateral lobes of *C. maculata* have more primary lateral veins (in mature specimens), seven to 10 pairs versus three to six pairs in *C. mirabilis*, with the veins aggregated in the basal one third in *C. maculata* and evenly distributed in *C. mirabilis*.

Chlorospatha maculata might also be confused with another species that occurs in Chocó, *C. chocoensis* (see discussion under *C. chocoensis*).

The two additional specimens cited are sterile and differ from the type. *M. Grayum et al.* 7634 dries gray-tinged green on both surfaces. The blades of

Croat 57304A are reported as thin and the petioles as soft. However, the leaves of both specimens are entirely green, with the blades matte on the upper surface and more primary lateral veins on all segments than are found in *C. mirabilis*, with those on the lateral lobes being aggregated in the basal one third.

In *Exotica 3* (Graf, 1963), a plant is pictured that is incorrectly identified as *Chlorospatha maculata*. The binomial, *C. maculata*, had not been published at that time and is being published here for the first time. The brief description of the plant indicates that the petiole and lower surface of the blade are purple, precluding the possibility that the pictured plant is *C. maculata*. The plant is of Colombian origin, according to the text, and is possibly *C. mirabilis*.

Paratypes. COLOMBIA. **Chocó:** Quibdó–Bolívar rd., 97 km E of Quibdó, near Km. 155, 500 m, 5°44'N, 76°27'W, 11 Mar. 1984, *Croat 57304A* (MO); Quebrada La Asquerosa, ca. 16 km beyond El Siete along Ciudad Bolívar–Quibdó rd., 825 m, 5°45'N, 76°22'W, 8 July 1986, *M. Grayum, B. Hammel, J. Kress & G. Brown 7634* (MO).

45. *Chlorospatha mansellii* Croat & L. P. Hannon, sp. nov. TYPE: Ecuador. Esmeraldas: Lita–San Lorenzo rd., 9.8 km W of old Río Lita bridge at Lita (prior to 1999), 701 m, 0°52'59"N, 78°30'49"W, 6 Mar. 1997, *L. P. Hannon 97-361* (holotype, MO-5291337!; isotypes, AAU!, B!, CAS!, COL!, CUVCI!, F!, HUA!, K!, MEXU!, NY!, RSA!, US!). Figures 35A–D, 36A, B.

Herba usque ad 60 cm; internodia 1–2.5 × 1.8–2.2 cm; cataphylla 12–26 cm longa. Petiolus 27–47 cm longus, vaginatus per 15–29 cm; lamina foliaris subhastata, 18.5–26 × 14–16 cm, lobis posterioribus 9–12 × 5.5–6.5 cm, nervis primariis lateralibus utroque 4 ad 6. Inflorescentiae 6 in quaque axilla; pedunculus 21–30 cm × 2–4(5) mm; spatha erecta, 9.5–12.2 cm × 7–10 mm; spadix 8.8–11 cm longus.

Terrestrial herb, to 60 cm tall; stem decumbent, erect 10–15 cm, remnants of old leaf bases persisting as a few short fibers at upper nodes; sap milky; internodes 1–2.5 × 1.8–2.2 cm, weakly glossy, pale to medium green, becoming brownish with age, drying matte, medium brown; cataphylls ultimately deciduous, 12–26 cm long, acuminate at apex, obtusely 1-ribbed and matte, medium green on outer surface, weakly glossy and conspicuously paler on inner surface, drying matte, medium brown. LEAVES 3 to 6, erect-spreading; **petioles** 27–47 cm long, glabrous, matte, medium to dark green, darkest and occasionally with a glaucous bloom toward base, drying matte to weakly glossy, medium to dark brown, rarely greenish, sheathed 15–29 cm, ca. 1/2 of total

length (rarely to 2/3); sheath decurrent at apex; free portion ca. 6 mm diam. midway, occasionally in part terete midway and otherwise in part or entirely obtusely D-shaped or U-shaped, broadly and obtusely sulcate, frequently with margins bluntly acute in apical 8–10 cm; **blades** held horizontally, weakly to moderately subhastate, usually hastate on drying, 18.5–26 × 14–16 cm, 1.2 to 1.8 times longer than wide, briefly acuminate to occasionally broadly acuminate at apex, broadest at base, 1 to 1.5 times wider at base than across anterior lobe (measured tip to tip across posterior lobes), frequently weakly to moderately constricted on one side in area of petiole attachment, thin, conspicuously bicolorous; upper surface weakly quilted, weakly glossy with a subvelvety sheen, medium to dark green, drying matte to weakly glossy, dark green or brownish green; lower surface reticulate, matte, and obscurely narrowly minutely colliculate along all orders of venation, otherwise weakly glossy to semiglossy, frequently yellowish, drying weakly glossy to semiglossy, moderately paler; anterior lobe 14–17.5 × 11.5–14.5 cm, 1.2 to 1.3 times longer than wide, 1.5 to 1.6 times longer than posterior lobes, broadest near base, ± symmetrical; posterior lobes directed somewhat outward, 9–12 × 5.5–6.5 cm, 1.6 to 2 times longer than wide, bluntly acute to narrowly rounded at apex, broadest at or near base, ± symmetrical, the inner side weakly to broadly rounded toward base, usually overlapping that of opposite lobe, obliquely attached or abruptly attenuate onto posterior rib, rarely decurrent onto petiole (on one side); outer side ± straight to weakly concave toward base; midrib and major veins weakly narrowly convex and weakly sunken on upper surface, weakly paler than surface, drying paler than surface, narrowly raised to round-raised on lower surface, matte, weakly paler than surface, drying weakly raised and ± flattened, concolorous to weakly darker than surface; **basal veins** 3 to 5 pairs, coalesced into a prominent posterior rib; posterior rib naked 3–10 mm per side (rarely not at all on one side); primary lateral veins 4 to 6 pairs, arising at 45°–55°, weakly to moderately arcuate; secondary veins in part obtusely sunken on upper surface, raised on lower surface, drying weakly raised, concolorous to weakly darker than surface; tertiary veins prominulous on lower surface, drying prominulous, concolorous to weakly darker than surface; reticulate veins entirely or in part prominulous and otherwise visible and distinct on lower surface, drying in part weakly prominulous, otherwise visible, distinct, concolorous to weakly darker than surface; collective veins 2 to 3, the innermost arising from one of the lowermost



Figure 35. *Chlorospatha mansellii* Croat & L. P. Hannon. —A. Paratype collection, *Croat et al.* 82143 (MO), plant removed from soil and leaning against roadside boulder. —B. Plant habit, showing adaxial blade surfaces. —C. Close-up of cultivated plant, with inflorescence at anthesis in frontal view at center. —D. Entire plant, with cultivar in flower. B–D photographed from the type collection *L. P. Hannon* 97-361 (MO).

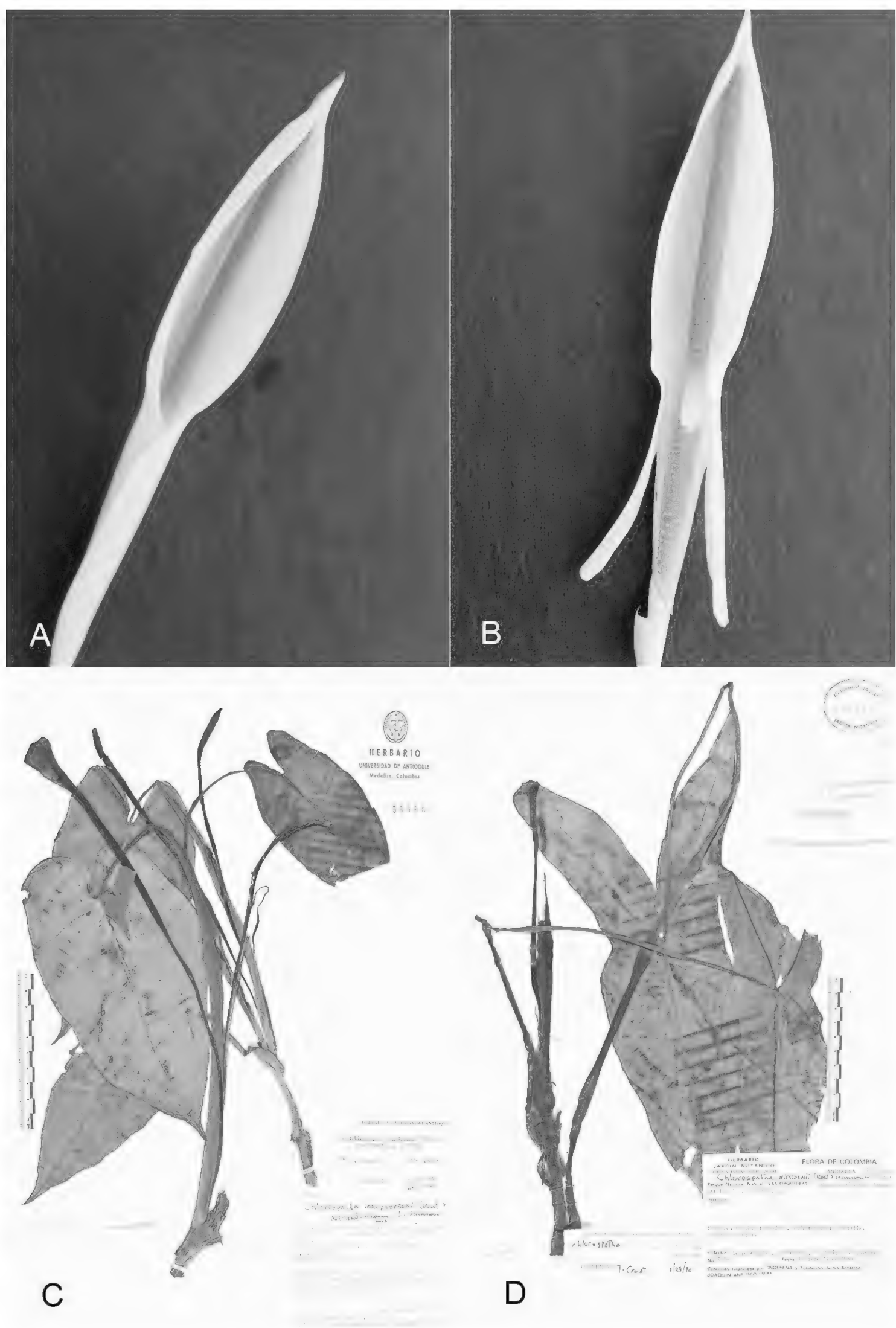


Figure 36. A, B. *Chlorospatha mansellii* Croat & L. P. Hannon, from the holotype L. P. Hannon 97-361 (MO). —A. Inflorescence near anthesis. —B. Inflorescence near anthesis, with spathe tube cut open. —C. *Chlorospatha macphersonii* Croat & L. P. Hannon, herbarium specimen *McPherson et al.* 12903 (HUA-58996). —D. *Chlorospatha nicolsonii* Croat & L. P. Hannon, herbarium specimen *Cogollo et al.* 3976 (JAUM-16944).

lateral veins on inner side of posterior lobe, loop-connected with all preceding lateral veins, weakly scalloped, 3–7 mm from margin. INFLORESCENCES erect, to 6 per axil, emitting a sweet or spicy-fruity fragrance at anthesis; peduncle held within the sheath, 21–30 cm \times 2–4(5) mm, thicker than broad, markedly so at apex (5 mm thick, 2 mm wide), occasionally broader than thick, narrowest toward base, matte to weakly glossy, pale green to pale yellow-green, drying matte to weakly glossy, medium-dark to dark green or brown; **spathe** erect, 9.5–12.2 cm long, lanceolate, \pm acute to weakly cuspidate at apex; spathe tube matte, greenish cream to pale yellowish green, narrowly paler at margins on outer surface, weakly glossy to glossy on inner surface, 4.2–6 cm \times 7–10 mm, thicker than broad, opening narrowly at apex at anthesis, drying matte, medium to dark (rarely pale) brown or greenish brown on outer surface, weakly glossy and weakly to moderately paler on inner surface; spathe blade weakly glossy to semiglossy, cream-colored, narrowly pale yellow-green medially on outer surface, matte on inner surface, 5.5–6.2 \times ca. 1 cm, to 3 cm wide at base (flattened), obtusely 1-ribbed abaxially (rib bluntly acute in apical 2 cm), drying matte to weakly glossy, occasionally in part semiglossy, brownish to greenish brown-cream on outer surface, matte on inner surface, opening broadly at anthesis, with margins narrowly out-rolled, marcescent, erect after anthesis; **spadix** erect, 8.8–11 cm long (slightly shorter than spathe), sessile, adnate to spathe ca. 2.6–4 cm at base, most or all of the length of pistillate portion; pistillate portion pinkish orange, 2.7–4 cm \times 3–4 mm, broadest toward apex, drying medium to dark pinkish to purplish brown; fertile staminate portion bright orange, 5–6 cm \times 4–5 mm, weakly thicker than broad, acute to bluntly acute at apex, broadest just above base, tapering, drying dark orangish brown; sterile staminate portion yellowish cream at base, yellowish orange toward apex, 5–10 \times 1.8–4 mm, cylindrical or weakly narrowest midway, drying cream to orangish brown; pistils weakly coherent, 4(5) across the axis (viewed from above), 1.2–1.6 mm long; ovaries white (drying creamy white), \pm subglobose, obtusely truncate at apex, 1.5–2 mm diam., 2(3)-locular, with axile placentation, 8 to 10 ovules per locule, hemianatropous, biseriate; funicles shorter than ovules; style Type 9 (Fig. 1), ca. 0.5 \times 1.5–2 mm, comprising 1/3 or less of the length of pistil, moderately broader than ovary apex, the margins \pm coherent with those of adjacent styles; red chromoplasts present; **stigma** white or cream, 0.5–0.7 mm diam., elevated on and weakly broader than narrowed portion of style; synandria 1–1.2 \times ca.

2 mm, coherent, truncate, deeply 3- to 4-lobed, 3- to 4-androus, with most flowers in apical 2 to 3 whorls lacking microsporangia; sterile flowers ca. 1 mm long, 2 \times 1 mm diam. and \pm elongated in direction of axis, coherent, truncate, irregularly subprismatic, in 5 to 8 whorls. Berries not known.

Phenology. Flowering is only known to occur in *Chlorospatha mansellii* during October and November. The species is known from only two sterile collections made in March and June, one of which later flowered in cultivation. Inflorescences are fragrant and emerge in slow progression, with several days between anthesis of one inflorescence and emergence of the next inflorescence at the apex of the petiole sheath. The cultivated specimen, observed over a period of six years, consistently flowered only during those two months.

Etymology. *Chlorospatha mansellii* is named for Dr. Richard Mansell, participant in several expeditions to Ecuador with the authors, and collaborator on the Flora of Ecuador and the Flora of Lita–San Lorenzo.

Discussion. *Chlorospatha mansellii* is known only from premontane wet forest on the western slopes of the Andes, in the vicinity of Lita in Esmeraldas Province in northern Ecuador, at 647–701 m elevation. The species is a member of *Chlorospatha* sect. *Occidentales*.

Chlorospatha mansellii might be confused with *C. besseae*, a sympatric species, also with *C. dodsonii*, which is sympatric with *C. mansellii* and *C. besseae* in the Lita–San Lorenzo region, with *C. mansellii* appearing to be intermediate between the two species and possibly a primary hybrid, sharing some intact characters of each as well as characters that would appear to be intermediate between those of the other two species (see discussions under *C. mansellii* and *C. besseae*).

The vegetative morphology of *Chlorospatha mansellii* also appears to be intermediate. The leaf blades of *C. dodsonii* are prominently hastate in both living and dried material, with the anterior and posterior lobes usually markedly constricted at the base and the posterior lobes usually about as long as the anterior lobe and acute at the apex. The blades of *C. besseae* are cordate, with the posterior lobes directed toward the base, not constricted, much shorter than the anterior lobe and rounded at the apex. In *C. mansellii*, the blades are intermediate, being weakly to moderately subhastate, constricted on one side or not at all, with the posterior lobes somewhat shorter than the anterior lobe and more or less acute at the

apex. Both *C. mansellii* and *C. besseae* have blades with four to five pairs of primary lateral veins, whereas those of *C. dodsonii* usually have six to eight pairs. In *C. mansellii* and *C. besseae*, the lower surface of the blade is narrowly colliculate along all abaxial venation, with the condition less pronounced in *C. mansellii* and more or less lacking in *C. dodsonii*. Consideration of all of the above poses the interesting possibility of hybridization in *Chlorospatha*, a phenomenon not previously explored or encountered.

Paratype. ECUADOR. **Esmeraldas:** Lita–San Lorenzo rd., 3.7 km W of old Río Lita bridge (below Lita, prior to 1999), 647 m, 0°52'51"N, 78°28'30"W, 30 June 1998, Croat, R. Mansell, L. P. Hannon & J. Whitehill 82143 (MO, QCNE).

46. *Chlorospatha mirabilis* (Mast.) Madison, Selbyana 5(3–4): 351. 1981. Basionym: *Xanthosoma mirabile* Mast. Gard. Chron., n.s. 1874(2): 258, tab. 53, 54. 1874. TYPE: Colombia. Tab. 53 in Masters, 1874: 258–259. Tropical South America, s.d., *B. Roezl s.n.*, cultivated by nurserymen Carter & Bull, at Kew Gardens (type, tab. 53 in Masters, 1874). Figures 37A, B, 38A.

Terrestrial herb, to 1.5 m tall; stem erect, in part subterranean, elongate, with remnants of old cataphylls persisting \pm intact at a few upper nodes; sap milky; internodes 5–12 mm \times 1–3 cm, scurfy brown, drying ca. 2 cm diam.; cataphylls ultimately deciduous, 17–25 cm long, obtuse with acumen at apex, purplish, obtusely 1-ribbed abaxially in apical 1/4 to 1/2, drying weakly glossy to semiglossy, medium-dark to dark reddish brown. LEAVES 1 to 3, erect-spreading; **petioles** (23–)33–96(–125) cm long, moderately spongy, glabrous, matte to weakly glossy, entirely dark purple or purple-tinged, or in part medium to dark olive-green in apical 1/3 to 2/3, occasionally with a glaucous bloom toward base, drying weakly glossy to semiglossy, dark brown to occasionally blackish brown, sheathed 30–69 cm, (1/3 to) 1/2 to 2/3 of total length; sheath decurrent or free-ending at apex, occasionally with sides minutely many-ribbed; free portion 6–12 mm diam. midway, subterete, obtusely or sharply flattened adaxially, with margins acute to acutely ribbed or obtuse throughout and acute toward apex, frequently 1-ribbed medially, rarely obtusely and shallowly sulcate in apical 1/3; **blades** deeply 3-lobed, rarely trisect, 30–54 \times 30–75 cm, 1 to 1.4 times wider than long, thinly coriaceous to subcoriaceous, moderately bicolorous; upper surface semiglossy to glossy, dark green, with or without irregular white, cream, yellowish, or pale green

maculations, drying weakly glossy to semiglossy, dark green or olive-green to brownish green or weakly reddish brown, the maculations weakly to moderately paler; lower surface weakly glossy to semiglossy, entirely purple to purple-violet, or green to yellow-green and entirely irregularly or moderately to heavily purple-tinged medially, drying semiglossy to glossy, weakly to moderately paler; **medial lobe** ovate to elliptic, (20–)27–44.5 \times 11–24 cm, 1.9 to 2.9 times longer than wide, (1 to) 1.2 to 1.5 times longer than lateral lobes, acute to weakly acuminate at apex, broadest at or below middle, cuneate (rarely weakly attenuate) toward and narrowly attached at base, 1.2–4.5 cm wide at point of attachment, \pm symmetrical, the margins rarely weakly sinuate; **lateral lobes** oblique or directed toward apex, (15.5–)22–42 \times (3.5–)6.5–20 cm, 1.7 to 3.6(to 4.3) times longer than wide, acute to weakly acuminate at apex, rarely bluntly acute, broadest at or below middle, usually markedly inequilateral, the inner side always narrower, long-attenuate (rarely straight) toward base, moderately to markedly narrowly confluent with medial lobe, confluent portion 2–5(–10) mm wide, rarely free to the base and not at all confluent; outer side 3 to 9 times wider than inner side midway, broadly rounded at base, occasionally weakly rounded, obliquely attached or abruptly attenuate onto posterior rib, rarely with a weakly developed auricle 7 \times 7 cm and narrowly rounded at apex; midrib and major veins usually purple on lower surface, drying \pm flattened; midrib obtusely to deeply sunken on upper surface, concolorous to weakly paler than surface, round-raised to narrowly rounded on lower surface, occasionally acutely angular on lateral lobes, drying moderately to prominently darker than surface; posterior rib naked 0.5–1.5(–2) cm per side; primary lateral veins (of all lobes) 3 to 6(7) pairs, arising at 30°–45°, weakly to moderately arcuate, occasionally straight, weakly to deeply sunken on upper surface, convex to round-raised on lower surface, occasionally purple-striped, drying weakly to prominently darker than surface; secondary veins obtusely sunken on upper surface, raised on lower surface, purple or green, drying \pm flattened, concolorous to weakly darker than surface, or entirely green and paler than surface; tertiary veins entirely prominulous or in part moderately or weakly raised and otherwise prominulous on lower surface, purple or green, drying in part weakly prominulous, otherwise flat, brownish and weakly darker than surface, or green and weakly paler than surface; reticulate veins obscure; collective veins 3, the innermost arising from one of the lowermost lateral veins at base, loop-connected with all preceding lateral veins, markedly scalloped (in mature specimens), 3–



Figure 37. *Chlorospatha mirabilis* (Mast.) Madison, cultivated accession at Munich, *E. Spear s.n.* (M). —A. Cultivated plant showing the maculation present on the adaxial leaf blade surface. —B. Cultivar, with the erect anthesal inflorescence emerging from the terminal axil below the trilobed, maculate blade. Photos by J. Bogner.

25 mm from margin. INFLORESCENCES erect, 3 or 4 per axil, emitting a weak, fruity fragrance at anthesis; peduncle held within the sheath, 30–59 cm \times 2–4 mm, trigonous or cylindroid and broader than thick, glossy, medium yellow-green most of length, matte to weakly glossy in apical 2.5 cm, drying matte to weakly glossy, dark brown to blackish brown; **spathe** erect, curved forward, (7–)8–15.5 cm long, acuminate or cuspidate at apex, cucullate at anthesis, acutely 1-ribbed in apical 1.5 cm abaxially, \pm tubular or narrowly funnel-shaped at anthesis and opening 2/3 to nearly 3/4 of its length, curved prominently forward post-anthesis; spathe tube matte or weakly glossy to glossy, medium green to yellow-green on outer surface, glossy to semiglossy on inner surface, moderately to prominently paler, rarely dark purple, (3.5–4)4.5–7.5 cm \times 6–10 mm, drying weakly glossy, medium green or dark brown to reddish brown on outer surface, usually weakly paler on inner surface, rarely dark purplish; spathe blade broadly elliptical (flattened), matte or weakly glossy to glossy, yellow, medium green to yellow-green, or whitish green on outer surface, matte and weakly paler on inner surface, (3–)4–7 \times ca. 1 cm, drying 6–7 mm diam., matte to weakly glossy,

tan to dark brown, opening \pm broadly at anthesis, with margins directed forward, in-rolled in apical 2.5 cm, marcescent, erect after anthesis; **spadix** erect, curved forward with spathe, (5.5–)6.5–10.1 cm long, sessile, adnate to spathe (1.2–)1.7–3.7 cm at base, ca. 1/2 to 3/4 of the length of pistillate portion; pistillate portion \pm ellipsoid, pink, pale yellow, cream, or pale orange, (2–)3–5 cm long, 3–6 mm diam. (dry), broadest at or just above middle, drying pink to orangish tan; fertile staminate portion white, greenish white, creamy tan or cream and weakly pink-tinged at anthesis (Croat & Mora 83686), (1.8–)2.6–3.6 cm \times 4–5 mm, \pm cylindrical, narrowly rounded at apex, weakly narrowed at base, drying pale yellow-tan to medium-dark or dark brown; sterile staminate portion greenish cream, (1.5–)1.7–2.4 cm \times 2–5 mm, \pm cylindrical or weakly broadest at base, drying creamy tan, rarely dark tan; pistils weakly coherent to \pm laxly arranged, or \pm densely arranged (Croat & Mora 83686), 4 to 6 across the axis (viewed from above), ca. 1.8–2.3 mm long; ovaries irregularly subcuboidal or cylindrical, (1–)1.5–2 mm diam., weakly narrower and truncate at apex, drying \pm white, dark purple at apex and irregularly purple along the sides, or frequently

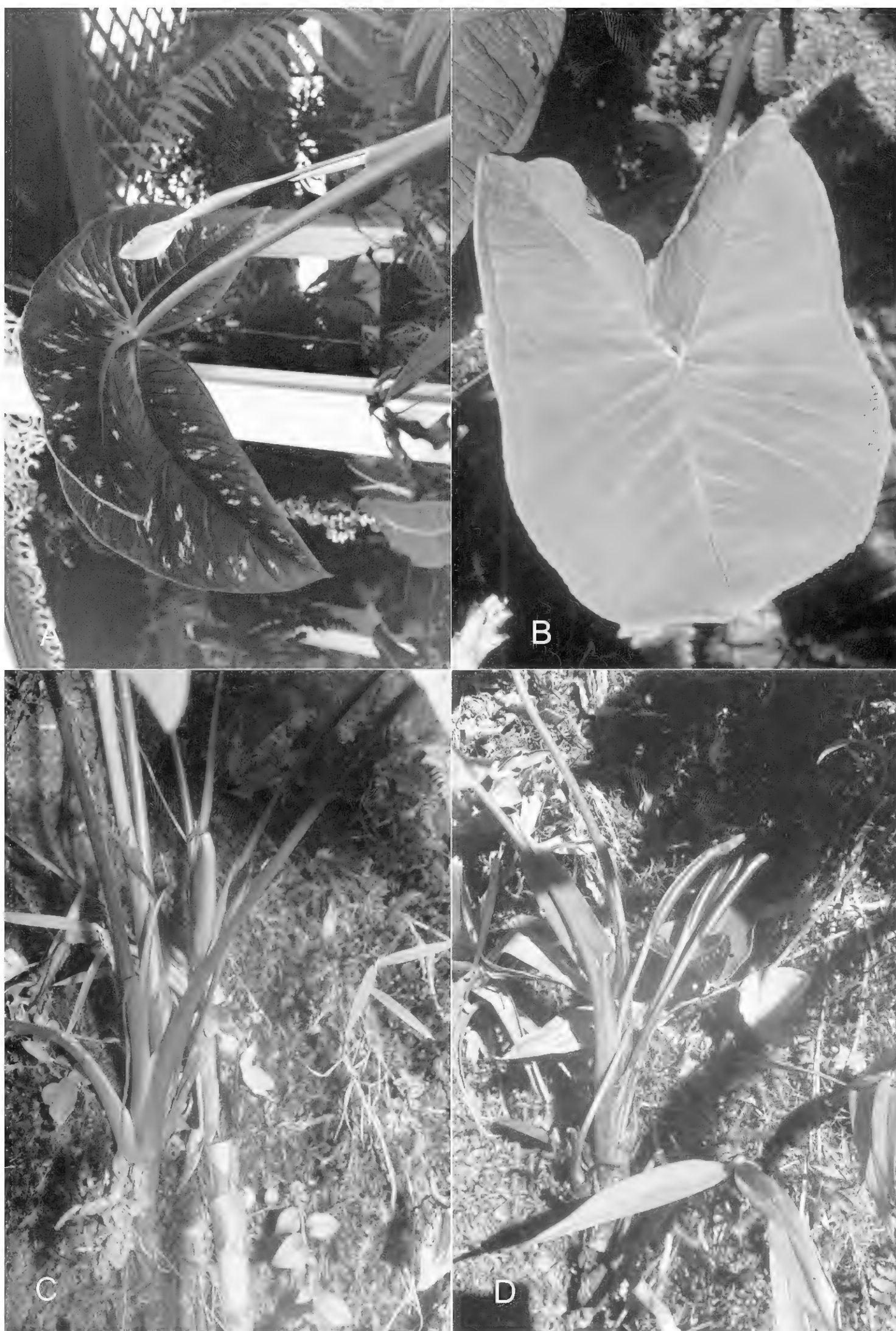


Figure 38. —A. *Chlorospatha mirabilis* (Mast.) Madison, *E. Spear s.n.* (M). Cultivated plant with inflorescence at anthesis. Photo by J. Bogner. B–D. *Chlorospatha munchiquensis* Croat & L. P. Hannon, from the holotype *Croat & Gaskin 80042* (MO). —B. Leaf blade adaxial surface. —C. Stems with pre-anthesis inflorescence. —D. Stem with four infructescences from the same axil.

entirely creamy white to creamy tan, with or without darker reddish veins, 3- to 4(5 to 6)-locular, with axile placentation (mainly in basal 2/3, *Croat & Mora 83686*); ovules numerous or 8 to 12 per locule (*Croat & Mora 83686*), biseriate, hemianatropous, micropyle superior; funicles longer than ovules; style Type 3 (Fig. 1), (1–)1.5–2 mm diam., weakly broader than ovary apex, rarely weakly narrower (*Croat & Mora 83686*), the margins irregularly weakly sinuate and weakly or not at all coherent with those of adjacent styles; **stigma** purplish or pink (*Croat & Mora 83686*), disklike, 0.5–1 mm diam., ca. 1/2 as wide as style, sessile, obtusely truncate, drying orangish tan; synandria, ca. 1–1.8 × 1–1.8 mm diam., frequently ± elongated in direction of axis in basal 2 to 4 whorls, coherent, truncate, deeply (2)3- to 4(5)-lobed, 3- to 4(5)-androus (mostly 3 or mostly 4 on different plants); pollen cream-colored; sterile flowers 0.2–0.5 mm long, (1–)2–3 × 1–1.5 mm diam. and ± elongated in direction of axis, laxly arranged (rarely weakly coherent), truncate, subprismatic, in 7 to 9(11) whorls, frequently drying with weakly darker brownish speckles. INFRUCTESCENCE dark green on outer surface, pale green on inner surface; berries pale green. JUVENILE plants with leaf blades entire, elliptical or frequently with small lobes at the base of medial lobe, or with well-developed lateral lobes weakly confluent with medial lobe.

Phenology. Flowering is only known to occur in *Chlorospatha mirabilis* during the months of February, April, June, July, and August.

Discussion. Prior to this treatment, *Chlorospatha mirabilis* was known only from the type, an illustration in *Gardeners' Chronicle*, and two herbarium specimens, none of which indicated a specific locality within tropical South America or Colombia. *Chlorospatha mirabilis* is known only from sea level to 900 m elevation in tropical rainforest and premontane rainforest on the western slopes of the Andes in Antioquia and Chocó departments, Colombia, and in transitional forest between tropical wet forest and premontane rainforest in Valle Department. The species also presumably occurs in southern Panama, in Darién Province, at 550–1400 m elevation, in tropical wet forest and premontane rainforest. As Madison (1981) rightly noted, the *Forget s.n.* collection sent from Peru was probably not collected in Peru, no collections of *C. mirabilis* having been made south of the aforementioned localities in Colombia. The collections from Panama are somewhat problematic, all being sterile and somewhat geographically isolated from the Colombian collections, with some from well above the elevations

recorded for most of the Colombian collections, however, and all appear to accord with *C. mirabilis*.

Chlorospatha mirabilis, a member of *Chlorospatha* sect. *Chlorospatha*, is a robust plant (to 1.5 m tall) distinguished by its deeply 3-lobed to nearly trisect and usually maculate leaf blades that are semiglossy to glossy on the upper surface and purple or purplish on the lower surface, with the petiole also purple. The species is also distinguished by its large inflorescence (to 15 cm long in mature specimens) with the sterile staminate portion of the spadix comprising about one third of the total length, an uncommon condition in *Chlorospatha*. The most densely arranged pistils in the genus were observed in one collection of the species, *Croat & Mora 83686*, wherein the ovaries of all flowers except those in a few apical and basal whorls were coherent most of their lengths, similar to those of *Xanthosoma*.

Chlorospatha mirabilis would be most easily confused with two species that also occur at low elevations in Chocó, *C. chocoensis* and *C. maculata*, and might eventually prove to be conspecific with one or both (see discussions under *C. chocoensis* and *C. maculata*). *Chlorospatha chocoensis* differs in having the petiole sheathed one third of its length, with the free portion terete; in *C. mirabilis*, the petiole is sheathed for a longer length, one half to two thirds, with its free portion sharply or obtusely flattened adaxially and the blades nearly almost trisect (rarely trisect). The posterior rib is naked 0.5–2 cm per side in *C. mirabilis*, but is not naked in *C. chocoensis*. The posterior rib is not naked and the blades in *C. mirabilis* are 3-lobed to nearly trisect (rarely trisect) and broadly confluent between segments (confluent portion 3.5–4 cm wide vs. less than 1 cm) in *C. mirabilis*, with the lateral segments only moderately inequilateral. The inflorescence of *C. chocoensis* is smaller, with the peduncles shorter (16–18 cm long vs. 30–59 cm in *C. mirabilis*). The spathe and spadix of *C. mirabilis* are longer, with the sterile staminate portion of the spadix comprising about one third of the total length (vs. one fourth in *C. chocoensis*), and the sterile flowers subprismatic. In *C. chocoensis*, the sterile flowers are fungiform and resemble toadstools (vs. cylindrical or weakly broadest at base in *C. mirabilis*), broadest at the apex and broadly concave medially, with deeply sinuate margins.

Chlorospatha mirabilis might be confused with *C. cogolloi* (see discussion under the latter Colombian species). The single collection of *C. mirabilis* cited from Antioquia, *Callejas et al. 6742*, appears to be somewhat intermediate between *C. mirabilis* and *C. cogolloi*. It was collected at higher elevations (approx. 900 m) north of the type locality of *C. cogolloi*, which

occurs only above 1200 m. All other Colombian collections of *C. mirabilis* were made at or below 150 m. *Callejas et al.* 6742 differs from the typical form of *C. mirabilis* in having the sterile staminate portion of the spadix comprising only one fourth of the total length, with the sterile flowers coherent, and therefore, possibly represents another taxon or an atypical specimen of *C. cogolloi*.

Chlorospatha maculata differs from *C. mirabilis* in having entirely green leaves, a brittle petiole, and subcoriaceous blades that are matte and not at all quilted on the upper surface, with the midrib and major veins only narrowly sunken. All segments are broadly concave on the upper surface (observed in photographs), a condition not previously observed in the genus, possibly resulting from the considerable thickness of the blade. The lateral lobes of *C. maculata* have more primary lateral veins (in mature specimens), seven to 10 pairs versus three to six pairs in *C. mirabilis*, with the veins aggregated in the basal one third in *C. maculata*, but evenly distributed in *C. mirabilis*.

It is noteworthy that all species with which *Chlorospatha mirabilis* might be confused are members of *Chlorospatha* sect. *Chlorospatha*. Among these is *C. ilensis*, known only from the western slopes of the Andes in Ecuador. There are no collections of either species, intermediate forms, or other species in section *Chlorospatha* in Ecuador.

The leaf blades of *Croat & Bay* 75777 and *Croat & Watt* 71002 differ from those of the other collections in lacking maculations. It is possibly significant that these and all other collections except *Hort. Veitch s.n.* have no purple in the spathe tube. *Croat & Watt* 71002 is distinctive in having the secondary and tertiary venation green on the lower surface, in both living and dried material, contrasting with the purple laminar surface. The blades of this collection dry only weakly bicolorous and the medial lobe is unusually narrow.

Additional specimens examined. COLOMBIA. S. loc., sent by Kalbreyer to Hort. Veitch, 17 Apr. 1882, s. coll. (K). **Antioquia:** Mpio. Frontino, La Blanquita distr., Murri region, 14.5 km W of Nutibara on Nutibara–La Blanquita rd., 890–900 m, *R. Callejas et al.* 6742 (HUA). **Chocó:** Serranía de Baudó, along Las Ánimas–Pató rd., on Río Pató, ca. 4 km SW of Pató, on property of Sr. Gutiérrez, 150 m, *Croat* 56133 (MO); vic. El Amargal, vic. Nuquí, 20–50 m, *Croat & Mora* 83686 (COL, MO, US) (= *Mora* 304 [COL, MO]); near jct. of Río Condoto & Río San Juan, 100–150 m, *E. Killip* 35091 (COL, US); Cabo Corrientes, Est. Biol. El Amargal, near sea level, *Mora* 161 (KKK, MO). **Valle:** Mpio. Buenaventura, Bajo Calima region, along Buenaventura–Málaga rd., Km. 51.3, less than 100 m, *Croat & Watt* 70380 (MO), 100 m, *Croat & Watt* 71002 (HUA, MO), Km. 51.7, 100 m, *Croat & Bay* 75777 (CUVC, MO); vic. of Bahía Málaga, Málaga Naval Base, Río Bongito, 40 m, *Croat &*

Watt 80503 (K, MO, US). PANAMA. **Darién:** middle slopes of W side of Cerro Pirre, 550–760 m, *Croat* 68888 (MO); Parque Nac. Darién, slopes of Cerro Mali, 22 km E of Púculo, 1300–1400 m, *H. Cuadros et al.* 3930 (MO); Parque Nac. Darién, near N & S branches of Río Púculo, N of Tacarcuna, 18 km E of Púculo, 600–800 m, *Hammel et al.* 16472 (MO). PERU.

Cultivated specimens examined. COLOMBIA. 1980, *E. Spear s.n.* (M).

47. *Chlorospatha morae* Croat & L. P. Hannon, sp. nov. TYPE: Colombia. Chocó: Mpio. Tadó, vic. Gingaraba, 26 Oct. 1991, *G. Lozano-C. & students* 6291 (holotype, COL-378032!). Figures 27D, 29D.

Herba ca. 1 m; internodia ca. $1 \times 0.8\text{--}2.5$ cm. Petiolus (20–)32–47 cm longus, vaginatus per 15–25 cm; lamina foliaris 5- ad 9-pedatisecta, $20\text{--}40 \times 27\text{--}48$ cm, lobo medio \pm elliptico, $18\text{--}25 \times 7\text{--}12$ cm, nervis primariis lateralis utroque 6 vel 7(8, 9). Inflorescentiae usque ad 4 in quaque axilla; pedunculus ca. $25 \text{ cm} \times 1\text{--}3 \text{ mm}$; spatha erecta ca. 3–7 cm longa, tubo 5–7 mm diam.; spadix ca. 5.5 cm longus.

Terrestrial herb, ca. 1 m tall (est.); stem erect, 15–50 cm tall, with remnants of old cataphylls persisting semi-intact and \pm fibrous at upper nodes, otherwise as loosely held, pale linear fibers (all measurements made from dried material); internodes ca. $1 \times 0.8\text{--}2.5$ cm, brown, drying matte, dark brown; cataphylls at least 19 cm long, apex not known, drying weakly glossy, dark reddish brown. LEAVES 2, erect-spreading; **petioles** (20–)32–47 cm long, glabrous, moderately to prominently minutely striate-ridged throughout, drying weakly glossy, dark brown to reddish brown, sheathed 15–25 cm, ca. 1/2 of total length; sheath decurrent at apex; free portion 3–5 mm diam. midway, entirely terete, or in part obtusely angular toward apex; **blades** 5- to 9-pedatisect, occasionally weakly alate between some segments, $20\text{--}40 \times 27\text{--}48$ cm, 1.2 to 1.3 times wider than long, thin to thinly coriaceous, moderately to prominently bicolorous; upper surface \pm bullate, matte to weakly glossy, dark green, drying weakly glossy, medium to dark brownish green, occasionally greenish brown; lower surface reticulate, matte to weakly glossy, drying semiglossy, occasionally weakly glossy, green, occasionally weakly gray-tinged, moderately to conspicuously paler; all segments \pm acute at base; **medial lobe** \pm elliptical, $18\text{--}25 \times 7\text{--}12$ cm, (2 to)2.3 to 2.9 times longer than wide, 1.1 to 3.5 times longer than lateral lobes, frequently weakly shorter than innermost lateral lobes, gradually or abruptly acuminate at apex, broadest midway, \pm symmetrical; **lateral lobes** $4.5\text{--}24.5 \times 1.5\text{--}12.5$ cm, 1.1 to 3.5 times longer than wide, gradually or abruptly

acuminate at apex, rarely acute, usually broadest at or below middle, occasionally above middle, progressively shorter and narrower toward outermost segments, with outermost segments usually much shorter and narrower than all other segments, progressively weakly to moderately inequilateral, most prominently so on outermost segments, the inner side always narrower; outer side 1.1 to 2.2 times wider than inner side midway, weakly to broadly rounded at base on outermost segments, rarely narrowly rounded, briefly attenuate onto posterior rib; all orders of venation sunken on upper surface, rarely with only the midrib and major veins sunken, usually prominently raised on lower surface; midrib occasionally paler than upper surface, round-raised and striate-ridged on lower surface, drying \pm raised, concolorous to moderately darker than surface; posterior rib naked 1.5–3.5 cm per side, round-raised on lower surface; primary lateral veins on all segments 6 to 7(8, 9) pairs (4 to 5 pairs on outermost segments), arising at 25° – 45° , moderately to markedly arcuate, prominently so toward apex, round-raised on lower surface, drying weakly raised to weakly flattened on lower surface, weakly to moderately darker than surface; secondary veins drying \pm raised on lower surface, weakly darker than surface; tertiary veins darker than lower surface, drying entirely \pm raised or in part prominulous, concolorous to weakly darker than surface; reticulate veins drying entirely weakly raised to prominulous on lower surface, or occasionally in part only visible and distinct, concolorous or weakly to moderately darker than surface; collective veins 2 to 3, the innermost arising from the lowermost lateral vein at the base, loop-connected with all preceding lateral veins, weakly to moderately scalloped, 2–10 mm from margin. INFLORESCENCES erect, to 4 per axil; peduncle held within the sheath, ca. 25 cm \times 1–3 mm, narrowest toward base, glabrous, drying weakly glossy, dark blackish brown; **spathe** erect, ca. 3–7 cm long, cuspidate at apex; spathe tube green, 3.5–4 cm \times 5–7 mm (2 cm \times 4 mm in immature inflorescence), drying weakly glossy, dark blackish brown; spathe blade white, 3.2 cm \times 4 mm, drying weakly glossy, dark brown; **spadix** erect, ca. 5.5 cm long, sessile, adnate to spathe 1–2 cm at base, ca. 1/2 of the length of pistillate portion; pistillate portion ca. 2.5–3 cm \times 4–6 mm (1.9 cm \times 2 mm on immature inflorescence), broadest midway; fertile staminate portion white, 2.5 cm \times 2–4 mm, narrowly rounded at apex, \pm clavate, drying medium brown; sterile staminate portion ca. 9 \times 1.5 mm, \pm cylindrical, drying medium brown; pistils weakly coherent, 3 to 4 across the axis (viewed from above), 1–1.5 mm long; ovaries subglobose, 1–2 mm diam.,

drying brownish; style Type 3 (Fig. 1C), ca. 1–1.5 mm diam., as broad as ovary apex, drying paler than ovary, the margins not coherent with those of adjacent styles; **stigma** 0.2–0.3 mm diam., sessile, disklike, obtusely truncate at apex, drying dark reddish brown; synandria ca. 1 \times ca. 1.2 mm, elongated in direction of axis in basal 3 whorls, deeply 3- to 4-lobed, 3- to 4-androus, coherent, truncate; sterile flowers ca. 0.5 mm long, 1–1.2 \times 0.75 mm diam. and \pm elongated in direction of axis, coherent, truncate, subprismatic, in 7 whorls. Berries not known.

Phenology. Flowering is only known to occur in *Chlorospatha morae* during the month of October.

Etymology. *Chlorospatha morae* is named for Marcela Mora Ward (1977–), graduate of the Universidad Nacional de Colombia, Bogotá, and specialist on the aroid flora of lowland Chocó Department, whose collection of *C. kolbii* made possible our understanding of that pivotal species. This new species is named in her honor, in recognition of her work on the Araceae of the Flora of Cabo Corrientes.

Discussion. *Chlorospatha morae* is known only from Chocó Department, Colombia, in premontane rainforest or transitional forest between tropical rainforest and premontane rainforest on the western slopes of the Cordillera Occidental at 285–825 m elevation. Most of the collections were made along the Medellín–Quibdó road west of Bolívar, very near the border with Antioquia Department. One collection, Croat 70881, was made on the border with Risaralda and the species would be expected to occur in that department and in Antioquia. Tadó, the type locality, is at approximately $5^{\circ}20'N$, $76^{\circ}40'W$ (est.), northeast of Istmina, on the road to Pueblo Rico.

Chlorospatha morae, a member of *Chlorospatha* sect. *Chlorospatha*, is an erect-growing species distinguished by its usually bullate, dark green, frequently prominently bicolorous, 5- to 9-pedatisect leaf blades with the segments relatively broad and elliptical, ovate or obovate, and acute and very narrowly attached at the base, with all venation usually sunken on the upper surface and raised or prominulous on the lower surface, with the lower surface reticulate. It is also distinguished by its small inflorescence with a green spathe tube and white blade.

Chlorospatha morae could be confused with only one species, *C. gentryi*, known only from the Parque Nacional Natural Las Orquídeas in Antioquia Department, Colombia, on the western slopes of the

Cordillera Occidental at higher elevations, 1200–1800 m (see discussion under *C. gentryi*).

Grayum (1986) originally filed *Croat 49311* and *Croat 55930*, sterile collections from Chocó Department, as *Chlorospatha croatiana* var. *enneaphylla*, possibly because of their 7-foliolate leaf blades and Colombian collection sites. Subsequent discovery of fertile material of *C. morae* indicates that these collections should be assigned to this species (cf. discussion under the latter species).

There is possibly more than one species involved in the collections cited here, all collections except the type being sterile. *Croat 49311* differs in drying with the minor venation more prominent. *Croat 70881* has only five segments, although it appears to be as mature as *Grayum et al. 7633*, which has nine segments. The type plant has seven segments. Both *Croat 70881* and *Grayum et al. 7633* dry paler, somewhat grayish green, whereas the type and other collections dry more brownish.

Paratypes. COLOMBIA. **Chocó:** along Medellín–Quibdó rd., 85 km W of Bolívar, 350 m, 11 Dec. 1979, *Croat 49311* (MO); along Quibdó–Medellín rd., Km. 159, 480 m, 13 Apr. 1983, *Croat 55930* (MO); along Quibdó–Medellín rd., at Km. 179, 20 km E of Tutunendo, 440 m, 5°44'N, 76°28'W, 22 Apr. 1983, *Croat 56303* (MO); Quibdó rd. from Bolívar, 97 km E of Quibdó, near Km. 155, 500 m, 5°44'N, 76°27'W, 11 Mar. 1984, *Croat 57286* (MO); along Pueblo Rico (Risaralda)–Istmina (Chocó) rd., 1 km W of Guarato & Río Guarato at Risaralda & Chocó border, 285 m, 5°21'N, 76°11'W, 22 Feb. 1990, *Croat 70881* (MO); along Quebrada La Asquerosa, along Bolívar–Quibdó rd., ca. 16 km beyond El Siete, 825 m, 5°45'N, 76°22'W, 8 July 1986, *M. Grayum, B. Hammel, J. Kress & G. Brown 7633* (MO).

48. *Chlorospatha munchiquensis* Croat & L. P. Hannon, sp. nov. TYPE: Colombia. Cauca: Parque Nac. Munchique, at Km. marker G1, 2 km W of summit, 2580 m, 2°30'38"N, 76°58'38"W, 19 July 1997, *Croat & J. Gaskin 80042* (holotype, MO-04940032!; isotype, CA-UP!). Figure 38B–D.

Herba minus quam 1 m; internodia 3–4 × usque ad 2.3 cm; cataphylla 9–18 cm longa. Petiolus 24–46 cm longus, vaginatus per 10.5–13.5 cm; lamina foliaris ovato-sagittata, 21–28 × 14–18 cm, lobis posterioribus 8.8–12 × (4–)4.5–9.5 cm, nervis basalibus utroque 4 ad 6, nervis primariis laterales utroque 6 ad 8. Inflorescentiae usque ad 4 in quaque axilla; pedunculus 13–15 cm × 2–3 mm; spatha erecta, longitudine ignota; spadix longitudine ignota, 6–8 mm diam.

Terrestrial herb, on steep bank, less than 1 m tall; stem decumbent, 40 cm long, with remnants of old cataphylls persisting ± intact along its length (usually entirely covering stem); internodes 3 to 4,

to 2.3 cm, semiglossy, olive-green, drying weakly glossy, dark reddish brown to blackish brown, occasionally irregularly finely transversely striate (all measurements made from dried material); cataphylls 9–18 cm long, obtuse with acumen at apex, 1-ribbed abaxially, green, drying weakly glossy to semiglossy, medium-dark reddish brown on outer surface, weakly paler on inner surface. LEAVES 3 to 5, erect-spreading; **petioles** 24–46 cm long, glabrous, semiglossy, brownish green, drying matte to weakly glossy, dark brown to blackish brown, sheathed 10.5–13.5 cm, ca. 1/3 or slightly more of total length; sheath free-ending at apex; free portion 3–5 mm diam. midway, terete; **blades** ovate-sagittate, subhastate in young plants, 21–28 × 14–18 cm, 1.5 to 1.6 times longer than wide, acuminate at apex, broadest at base, 1.1 to 1.5 times wider at base than across anterior lobe (measured tip to tip across posterior lobes), weakly to moderately constricted in area of petiole attachment, with one side ca. 2 cm wider than opposite side, subcoriaceous, weakly bicolorous; upper surface weakly bullate, velvety-matte, dark green, drying matte, dark brown; lower surface weakly glossy, drying weakly glossy to in part semiglossy, weakly paler; anterior lobe 14–19 × 9.3–17 cm, 1 to 1.7 times longer than wide, 1.4 to 1.6 times longer than posterior lobes, broadest at or below middle, weakly inequilateral, with one side 1–1.5 cm wider than opposite side midway; posterior lobes directed toward the base, somewhat outward in young plants, 8.8–12 × (4–) 4.5–9.5 cm, 1.3 to 2.3(to 2.5) times longer than wide, narrowly rounded to bluntly rounded or bluntly acute at apex, broadest at base or weakly broadest below middle, weakly to moderately inequilateral, the inner side narrower, weakly to broadly rounded toward base, decurrent onto petiole (onto posterior rib in young plants, with rib naked 5 mm per side); outer side 1 to 1.4 times wider than inner side midway, ± straight to weakly concave toward base; sinus 7.5–10.5 cm deep, oblong to spatulate, or broadly V-shaped, occasionally with lobes overlapping; midrib and major venation deeply sunken on upper surface, round-raised on lower surface, drying raised to weakly flattened, weakly darker to weakly paler than surface; **basal veins** 4 to 6 pairs, coalesced into prominent posterior rib; primary lateral veins 6 to 8 pairs, arising at 50°–65° on broad side, 35°–45° on narrow side, weakly arcuate, rarely irregularly ascending; secondary and tertiary veins sunken on upper surface, prominently raised on lower surface, drying raised, occasionally in part prominulous, weakly or prominently darker than surface; reticulate veins drying in part distinct and flat on lower surface, rarely in part weakly prom-

inulous, concolorous to weakly darker than surface; collective veins 3, the innermost arising from one of the lowermost lateral veins on the inner side of the posterior lobe, loop-connected with all preceding lateral veins, \pm parallel to and 3–7 mm from margin. INFLORESCENCES erect, to 4 per axil; peduncle held within the sheath, 13–15 cm \times 2–3 mm, drying matte to weakly glossy, medium-dark to dark brown; **spathe** erect, total length and apex not known; spathe tube dark green and dark purple-tinged on outer surface, dark purple on inner surface; spathe blade not known; **spadix** total length not known, sessile, adnate to spathe 6–8 cm at base, the entire length of pistillate portion; pistillate portion not known; fertile staminate portion not known; sterile staminate portion ca. 7 \times 1.5–2 mm, drying dark reddish brown; pistils not known; style probably attenuate, with the stigma \pm elevated on narrowed portion; synandria ca. 1 \times ca. 1.5 mm, 4-lobed, 4-androus, coherent, truncate (2 flowers examined); sterile flowers ca. 0.8 mm long, 1.5–2 \times 1 mm diam. and \pm elongated in direction of axis, coherent, truncate, irregularly subprismatic, in 3 to 4 whorls. INFRUCTESCENCE 6.2–8.5 cm \times 6–9 mm, drying matte to weakly glossy, dark brown on outer surface, moderately paler on inner surface; berries 3–5 mm diam., drying tan.

Phenology. Flowering and fruiting are only known to occur in *Chlorospatha munchiquensis* during the month of July.

Etymology. *Chlorospatha munchiquensis* is named for the type locality, Parque Nacional Munchique, located along the crest of the Cordillera Occidental in Cauca Department of Colombia.

Discussion. *Chlorospatha munchiquensis* is known only from the type collection made in Parque Nacional Munchique on the western slopes of the Cordillera Occidental in Cauca Department, Colombia, 2 km west of the summit of the Continental Divide, at Km. marker G1, at 2580 m elevation. The species occurs in premontane wet forest and lower montane wet forest and would be expected to occur elsewhere within the department, in suitable habitat, possibly on the eastern slopes.

Chlorospatha munchiquensis is a member of *Chlorospatha* sect. *Occidentales* and is distinguished by its weakly bullate, broadly ovate-sagittate leaf blades that are weakly to moderately constricted in the area of petiole attachment, velvety-matte and dark green on the upper surface, only weakly bicolorous, and dry dark brown. All venation except the reticulate is prominently raised on the lower surface, and, in some specimens, the secondary and tertiary

veins dry conspicuously darker than the surface, giving the blades a distinctive appearance.

Chlorospatha munchiquensis could possibly be confused with *C. macphersonii* from the eastern slopes of the Cordillera Occidental, in the vicinity of Jardín at the southern end of Antioquia Department, near the border with Caldas and Risaralda departments, at almost 3000 m elevation (see discussion under *C. macphersonii*).

49. *Chlorospatha nambiensis* Croat & L. P. Hannon, sp. nov. TYPE: Colombia. Nariño: Mpio. Barbacoas, Altaquér distr., vic. El Barro, Res. Nat. Río Nambí, rt. bank of Río Nambí, 1325 m, 1°18'N, 78°08'W, 8 Dec. 1993, P. Franco, D. Giraldo, W. Beltrán, A. Prieto & O. Rivera 5056 (holotype, COL-360481!). Figure 39A.

Herba 60–80 cm; internodia 1.2–2 \times 1.2–1.7 cm; cataphylla ultra 10 cm longa. Petiolus 34–48.5 cm longus, vaginatus per 8–12.5(–19.5) cm; lamina foliaris hastata, 18.5–27.5 \times 23–25 cm, lobis posterioribus 12.5–13.5 \times 3.5–5 cm, nervis basalibus utroque 6 ad 8, nervis primariis lateralibus utroque 3 vel 4(5). Inflorescentiae usque ad 3 in quaque axilla; pedunculus 10.2–13 cm \times 1–2 mm; spathe longitudine ignota sed existimata ca. 6–6.5 cm, ca. 5 mm diam., lamina ca. 3 cm \times 7 mm; spadix ca. 6.1 cm longus.

Terrestrial herb, 60–80 cm tall; stem with remnants of old leaf bases persisting semi-intact at some uppermost nodes (all measurements made from dried material); internodes 1.2–2 \times 1.2–1.7 cm, drying matte, dark brown; cataphylls ultimately deciduous, more than 10 cm long, total length and apex not known, drying weakly glossy, medium-dark reddish brown, \pm fibrous. LEAVES 2, erect-spreading; **petioles** 34–48.5 cm long, glabrous, pale green, drying matte, medium-dark to dark brown, sheathed 8–12.5(–19.5) cm, ca. 1/3 of total length; sheath maroon, decurrent at apex; free portion 2–3 mm diam. midway; **blades** hastate, 18.5–27.5 \times 23–25 cm, 1.1 times longer than wide, or frequently to 1.2 times wider than long, gradually to abruptly acuminate at apex, broadest at base, 2.7 to 3 times wider at base than across anterior lobe (measured tip to tip across posterior lobes), thin (dry), moderately bicolorous; upper surface green, drying matte, dark brown, with densely dispersed, pale, punctiform, and short, linear raphid cells; lower surface drying weakly glossy, occasionally in part semiglossy, weakly paler or concolorous; anterior lobe 12.7–20 \times 8–8.6 cm, 1.6 to 2.3 times longer than wide, 1 to 1.5 times longer than posterior lobes, broadest near base or midway, weakly to markedly constricted at base, occasionally not at all on one side, weakly inequilateral, with one side 1.1 to 1.5 times wider than

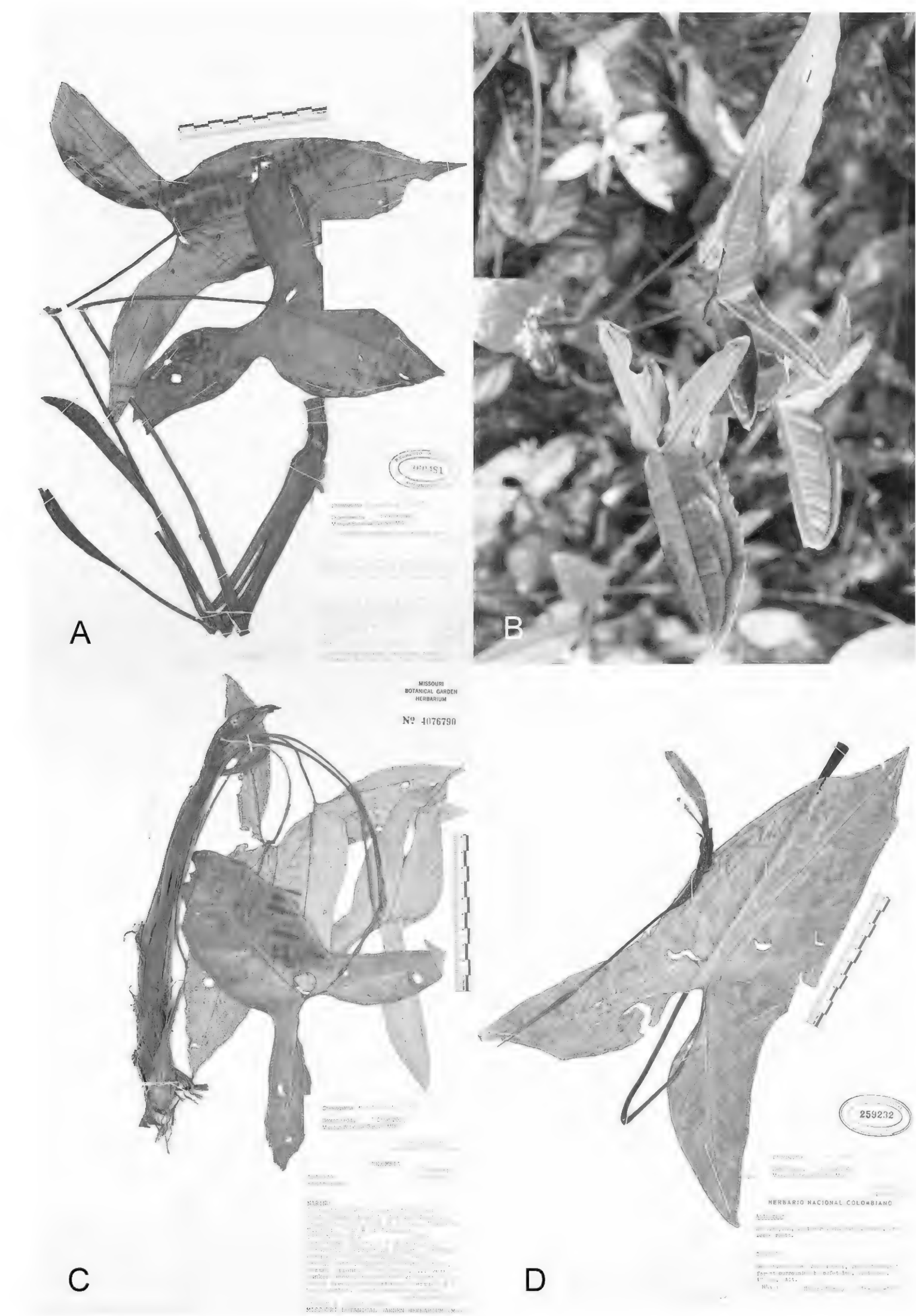


Figure 39. —A. *Chlorospatha nambiensis* Croat & L. P. Hannon, the holotype *Franco et al.* 5056 (COL-360481). B, C. *Chlorospatha narinoensis* Croat & L. P. Hannon, the holotype *Croat* 72398 (MO). —B. Plant habit, showing adaxial surfaces of blades. —C. Holotype specimen (MO-4076790). —D. *Chlorospatha noramurphyae* Croat & L. P. Hannon, the isotype *Murphy* 383 (COL-259232).

opposite side; posterior lobes directed prominently outward, $12.5\text{--}13.5 \times 3.5\text{--}5$ cm, 2.6 to 3.8 times longer than wide, narrowly rounded to bluntly acute at apex, broadest below middle, usually markedly constricted at base, 1.4 to 2.3 times wider at widest point than at point of constriction, \pm symmetrical to weakly inequilateral, the inner side broadly rounded and markedly narrowly long-attenuate toward base, the attenuate portion less than 1 mm wide, decurrent onto posterior rib; outer side \pm straight toward base; midrib, major and secondary venation drying moderately darker than lower surface; midrib round-raised on lower surface, drying raised; **basal veins** 6 to 8 pairs, coalesced into a prominent posterior rib; posterior rib naked 3–10(–12) mm per side; primary lateral veins 3 to 4(5) pairs, arising at $25^\circ\text{--}50^\circ$, most acutely toward apex, straight, weakly to markedly arcuate or irregularly ascending, convex on lower surface, drying raised near base, otherwise \pm flattened; secondary veins raised on lower surface, drying raised; tertiary veins drying prominent on lower surface, darker than surface; reticulate veins drying obscure; collective veins 3, the innermost arising from one of the lowermost lateral veins on the inner side of the posterior lobe, loop-connected with all preceding lateral veins, moderately scalloped, 2–10 mm from margin. INFLORESCENCES erect, to 3 per axil; peduncle held within the sheath, $10.2\text{--}13$ cm \times 1–2 mm (ca. 18 cm \times 3.5 mm when in fruit), pale green, drying matte, dark brown; **spathe** habit not known, ca. 6–6.5 cm long (est.), apex not known; spathe tube cream-colored, 3–4 cm \times ca. 5 mm, drying matte, in part weakly glossy, dark brown on outer surface, matte to weakly glossy, and weakly paler on inner surface, with regularly rounded, pale cellular inclusions, the inclusions concentrated in medial 1/3; spathe blade cream or white, ca. 3 cm long, 7 mm wide (flattened), drying matte, dark brown on outer surface, weakly glossy on inner surface, marcescent, erect after anthesis; **spadix** erect, curved weakly forward, ca. 6.1 cm long, sessile, adnate to spathe ca. 3–3.5 cm at base, the entire length of pistillate portion and onto sterile staminate portion 1.5 mm; pistillate portion 2.8–3.5 cm \times 2–3 mm, broadest midway, drying dark, reddish brown; fertile staminate portion brown, ca. 2.2 cm \times ca. 3 mm, \pm cylindrical, narrowly rounded at apex, drying dark reddish brown; sterile staminate portion ca. 1.2 cm \times 2 mm, weakly broadest at apex, drying dark reddish brown; pistils weakly coherent, 3 to 4 across the axis (viewed from above), ca. 1.8 mm long; ovaries subglobose, ca. 2 mm diam.; style Type 8 (Fig. 1), $1 \times 1.2\text{--}1.3$ mm (attenuate portion ca. 0.7 mm long), comprising ca. 1/2 of the length of pistil, weakly

broadly than ovary apex, the margins weakly coherent with those of adjacent styles; **stigma** 0.2–0.3 mm diam., markedly elevated on and weakly broader than narrowed portion of style; synandria ca. $1 \times 0.8\text{--}1.4$ mm, coherent, truncate, 3- to 4-lobed, 3- to 4-androus; sterile flowers 0.6–0.8 \times 0.5–0.8 mm, or 0.4–0.8 \times 1–1.8 mm diam. and \pm elongated in direction of axis, fungiform (like toadstools) in basal 4 to 5 whorls and markedly laxly arranged (with only 5 to 6 flowers present), several-branched or markedly irregularly and deeply lobed in apical 2 to 4 whorls and weakly coherent, the branches truncate, broadest at and abruptly narrowing below apex. INFRUCTESCENCE cream-colored, 7–9.5 cm \times 9–13 mm, drying matte, dark brown; berries (immature) 2–3 mm diam.

Phenology. Flowering and fruiting are only known to occur in *Chlorospatha nambiensis* during the month of December.

Etymology. *Chlorospatha nambiensis* is named for the Reserva Natural Río Nambí in Nariño Department of Colombia, where the type was collected.

Discussion. *Chlorospatha nambiensis* is known only from premontane wet forest on the western slopes of the Cordillera Occidental, in the Reserva Natural Río Nambí in Nariño Department, Colombia, at 1325 m elevation. The species would be expected to occur elsewhere in the department and southward into northern Ecuador, in suitable habitat.

Chlorospatha nambiensis is a member of *Chlorospatha* sect. *Occidentales* and is distinguished by its hastate, dark brown-drying leaf blades with all lobes usually prominently constricted at the base, the posterior lobes narrow and as long as or moderately shorter than the anterior lobe and the inner margins conspicuously long-attenuate toward the base. The lower surface of the blade dries concolorous to weakly paler than the upper surface, with the major and secondary venation darker than the surface. The petiole is pale green and sheathed one third of its length, with the sheath maroon. *Chlorospatha nambiensis* is also characterized by its short, pale green peduncle, one third as long as the petiole, and small inflorescence with the spathe less than 7 cm long and usually entirely cream-colored. The sterile staminate portion of the spadix comprises one fifth of the total length and is markedly laxly flowered in the basal one half, with only five to six flowers on the axis. The synandria are reported as brown.

Chlorospatha nambiensis would be most easily confused with *C. narinoensis*, with which it is possibly sympatric in Nariño Department. Both species have

the petiole sheathed one third of its length, hastate leaf blades (on drying) with pale raphid cells on the upper surface, long posterior lobes, short peduncles, and small inflorescences.

Chlorospatha nambiensis differs in having the petiole sheath maroon and the leaf blades drying dark brown, not at all greenish, with the midrib, major, and minor venation drying darker than the lower surface and the major venation flattened. In *C. narinoensis*, the petiole sheath is green and the leaf blades dry green or greenish, with the venation concolorous to weakly paler than the lower surface and the major venation raised. In *C. nambiensis*, the fertile staminate portion of the spadix is brown; the style (Type 8, Fig. 1) is appressed to the ovary (not broadly spreading); and the sterile flowers are fungiform to branched and laxly arranged, markedly so in the basal half of the sterile portion. In *C. narinoensis*, the fertile staminate portion is cream-colored; the style (Type 5, Fig. 1) is broadly spreading; and the sterile flowers are subprismatic and densely arranged. The species are possibly closely related.

Chlorospatha nambiensis could possibly be confused with *C. carchiensis* from the western slopes of the Andes, in the vicinity of Maldonado in Carchi Province, Ecuador, at 1740–1800 m elevation. The species could ultimately prove to be sympatric, their type localities being in close proximity. The petiole is sheathed one half or slightly more of its length, the sheath is green and free-ending at the apex, and the leaf blades are sagittate with broad posterior lobes (see discussion under *C. carchiensis*).

Paratype. COLOMBIA. **Nariño:** Mpio. Barbacoas, Altaquér distr., vic. El Barro, Res. Nat. Río Ñambí, lt. bank of Río Ñambí, 1325 m, 1°18'N, 78°08'W, 10 Dec. 1993, *P. Franco et al.* 5132 (COL).

50. *Chlorospatha narinoensis* Croat & L. P. Hannon, sp. nov. TYPE: Colombia. Nariño: along trail leading from main Pasto–Tumaco rd. to Río Ñambí, departing main rd. at Escuela Mixta El Mirador, 7 km W of Altaquér, 1100 m, 1°18'N, 78°04'W, 26 Feb. 1992, *Croat* 72398 (holotype, MO-4076790!; isotypes, K!, PSO!). Figure 39B, C.

Herba 0.5–1.6 m; internodia 1–1.5 × 1.2–1.8 cm; cataphylla 11–16 cm longa. Petiolus 36–46 cm longus, vaginatus per 8–13.5 cm; lamina foliaris hastata, 15.5–27 × 14.5–27 cm, lobis posterioribus 10.2–16 × 2.2–3.7(–4.4) cm, nervis basalibus utroque (5)6 vel 7, nervis primariis lateralibus utroque 3–5. Inflorescentiae erectae, usque ad 3 in quaque axilla; pedunculus 12–14.5 cm × 1–3 mm; spatha erecta, 6–7.5 cm longa, tubo 4–5 mm diam., lamina 3–3.5 cm × ca. 5 mm; spadix 5–6 cm longus.

Terrestrial herb, 0.5–1.6 m tall; stem with remnants of old cataphylls persisting ± intact at upper nodes, weakly fibrous; sap milky; internodes 1–1.5 × 1.2–1.8 cm, green, drying matte, medium-dark brownish green (all measurements made from dried material); cataphylls 11–16 cm long, ± obtuse with acumen at apex, 1-ribbed abaxially, drying semiglossy to glossy, medium to dark reddish brown. LEAVES 1 to 4, erect-spreading; **petioles** 36–46 cm long, glabrous, matte, medium green, drying matte to weakly glossy, medium-dark to dark brown, sheathed 8–13.5 cm, ca. 1/3 or less of total length; sheath decurrent at apex; free portion 1.5–4 mm diam. midway, obtusely angular adaxially; **blades** held ± horizontally, the apices of all lobes directed ± upward, hastate (rarely subhastate on drying), 15.5–27 × 14.5–27 cm, 1 to 1.3(to 1.8) times longer than wide, acuminate at apex, broadest at base, (2.7 to)3.4 to 4.2 times wider at base than across anterior lobe (measured tip to tip across posterior lobes), moderately to markedly constricted in area of petiole attachment, thin, weakly to moderately bicolorous; upper surface quilted, matte, dark green, drying matte, medium-dark green to brownish green, with densely dispersed, pale, punctiform and short linear raphid cells; lower surface matte to weakly glossy, drying weakly glossy to semiglossy, weakly to moderately paler; anterior lobe 12.7–19 × 4.5–8(–9.5) cm, (1.8 to)2.4 to 2.8 times longer than wide, 1.2 to 1.3(to 1.5) times longer than posterior lobes, broadest near base, moderately to markedly constricted at base, ± symmetrical; posterior lobes directed prominently outward, 10.2–16 × 2.2–3.7(–4.4) cm, (2.6 to)4 to 4.6 times longer than wide, narrowly rounded to bluntly acute at apex, broadest midway, usually markedly constricted at base, (1.3 to)1.6 to 2.3 times broader midway than at point of constriction, ± symmetrical, the inner side weakly rounded and narrowly long-attenuate toward base, rarely abruptly attenuate; outer side ± straight toward base; major and secondary venation quilted-sunken on upper surface, raised on lower surface, drying raised, concolorous to weakly paler than surface; midrib deeply sunken on upper surface, round-raised on lower surface, weakly paler than surface; **basal veins** (5)6 to 7 pairs, coalesced into a prominent posterior rib, the first free to the base; posterior rib naked 3–8 mm per side, narrowly raised or round-raised on lower surface; primary lateral veins 3 to 5 pairs, arising at 35°–65°, weakly arcuate to irregularly ascending, convex on lower surface; secondary veins raised on lower surface; tertiary veins in part sunken on upper surface, raised on lower surface, drying entirely or in part prominulous

and otherwise distinct; reticulate veins drying obscure; collective veins 3, the innermost arising from one of the lateral veins on the inner side of the posterior lobe, loop-connected with all preceding lateral veins, weakly scalloped, 3–7 mm from margin. INFLORESCENCES erect, to 3 per axil; peduncle held within the sheath, 12–14.5 cm \times 1–3 mm (to 16 cm long when in fruit), pale green, drying matte, medium to dark brown; **spathe** erect, 6–7.5 cm long, abruptly acuminate at apex; spathe tube pale green or white, 3–4 cm \times 4–5 mm, drying matte, dark brown on both surfaces; spathe blade white, 3–3.5 cm \times ca. 5 mm, ca. 1.5 cm wide (flattened), 1-ribbed abaxially, drying matte, dark reddish brown on both surfaces, weakly paler than tube, marcescent, erect after anthesis; **spadix** erect, 5–6 cm long, sessile, adnate to spathe 1.8–3.2 cm at base, most or all of the length of pistillate portion; pistillate portion 2.2–3.2 cm \times ca. 2 mm, broadest toward apex, drying dark reddish brown; fertile staminate portion cream-colored, 1.6–2.3 cm \times 2–3 mm, weakly clavate, narrowly rounded at apex, drying medium-dark yellowish brown, occasionally weakly gray-tinged; sterile staminate portion 5–8 \times 1.5–2 mm, \pm cylindrical, drying dark reddish brown; pistils weakly coherent, 2 to 4 across the axis (viewed from above), 1.7–2 mm long; ovaries subglobose, 1.5–1.7 mm diam.; style Type 5 (Fig. 1), 0.8–1.2 \times 1–1.5 mm (attenuate portion ca. 1 mm long), comprising ca. 1/2 of the length of pistil, broader than ovary apex, the margins frequently \pm coherent with those of adjacent styles; **stigma** 0.3–0.5 mm diam., markedly elevated on and broader than narrowed portion of style; synandria ca. 1 \times ca. 1 mm, coherent, truncate, (2)3- to 4-lobed, (2)3- to 4-androus (mostly 3); sterile flowers ca. 0.5 mm long, 1–2 \times 0.5–1 mm diam. and \pm elongated in direction of axis, coherent to weakly coherent, truncate, subprismatic to irregularly lobed, in 4 to 5 whorls. INFRUCTESCENCE ca. 7.5 \times 1.2 cm; berries pale greenish yellow, 4–5 mm diam.

Phenology. Flowering is only known to occur in *Chlorospatha narinoensis* during the months of February and December, with fruiting reported for February.

Etymology. *Chlorospatha narinoensis* is named for Nariño Department of Colombia, where the species is endemic.

Discussion. *Chlorospatha narinoensis* is known only from premontane wet forest on the western slopes of the Cordillera Occidental, near the Reserva Natural Río Ñambí in Nariño Department, Colombia, at 1100–1325 m elevation. The species would be

expected to occur elsewhere within the department, also southward into Carchi Province in northern Ecuador and possibly to the north in Cauca Department.

Chlorospatha narinoensis is a member of *Chlorospatha* sect. *Occidentales* and is distinguished by its hastate, matte, dark green leaf blades with the anterior and posterior lobes moderately to markedly constricted at the base, and the posterior lobes narrow and almost as long as the anterior lobe. The species is also distinguished by its petiole, which is obtusely angular in the free portion and sheathed one third of its length, with the peduncle accordingly short (12–14.5 cm long) and the inflorescence small, 6–7.5 cm long. The style comprises one half or more of the length of the pistil, with the attenuate portion markedly long (1 mm long) and the mantle much broader than the ovary apex.

Chlorospatha narinoensis could be most easily confused with *C. nambiensis*, with which it is possibly sympatric in Nariño Department. Both species have the petiole sheathed one third of its length, hastate leaf blades (on drying) with pale raphid cells on the upper surface, long posterior lobes, short peduncles, and small inflorescences (see discussion under *C. nambiensis*).

Chlorospatha narinoensis could possibly be confused with *C. carchiensis* from the western slopes of the Andes, in the vicinity of Maldonado in Carchi Province, Ecuador, at 1740–1800 m elevation. The species could ultimately prove to be sympatric; their type localities being in close proximity (see discussion under *C. carchiensis*).

Betancur et al. 4872 is possibly a different species. It differs vegetatively from the other collections in having sagittate, brown-drying leaf blades with the posterior lobes proportionally broader and less constricted at the base. The anterior lobe is also broader relative to its length. The spathe is reported as entirely white, thus differing from the other collections in which the spathe tube is pale green and the blade white. However, the percentage of sheathing on the petiole, the peduncle length, and floral morphology appear to accord with the type, and the collection was made at the type locality.

Paratypes. COLOMBIA. **Nariño:** Mpio. Barbacoas, Altaquer distr., vic. El Barro, Res. Nat. Río Ñambí, on lt. side of Río Ñambí, 1325 m, 1°18'N, 78°08'W, 11 Dec. 1993, *J. Betancur 4816* (COL), *Betancur, A. Guzman, R. Lopez & S. Vargas 4872* (COL).

51. *Chlorospatha nicolsonii* Croat & L. P. Hannon, *Aroideana* 27: 34. 2004. TYPE: Colombia. Antioquia: trail from Encarnación to Parque Nac. Nat. Las Orquídeas, 1600–1800 m, 27 Jan.

1979, A. Gentry & E. Rentería 24590 (holotype, MO-2715459!; isotype, COL!). Figure 36D.

Terrestrial or hemiepiphytic herb, to ca. 1 m tall; stem decumbent, with remnants of old leaf bases and cataphylls persisting \pm intact and weakly fibrous at upper nodes (all measurements made from dried material); internodes 2–4 cm \times 8–10 mm, drying weakly glossy, dark brown, occasionally finely irregularly transversely ridged, ridges darker than surface; cataphylls ca. 16–19 cm long, apex not known, drying weakly glossy to semiglossy, dark reddish brown, weakly fibrous. LEAVES 2 to 3, erect-spreading; **petioles** 38–60 cm long, drying glabrous, semiglossy, dark reddish brown, sheathed 15–22 cm, ca. 1/3 of total length; sheath decurrent at apex; free portion 3–5 mm diam. midway; **blades** subhastate, 28–35 \times 18–22 cm, 1.7 to 2.2 times longer than wide, acute to acuminate at apex, broadest at base, 1.9 to 2.8 times wider at base than across anterior lobe (measured tip to tip across posterior lobes), weakly to moderately constricted in area of petiole attachment, drying thinly coriaceous, concolorous to moderately bicolorous; upper surface drying matte to weakly glossy, occasionally in part semiglossy, dark brown to greenish brown; lower surface drying weakly glossy to semiglossy; anterior lobe 18–20.5 \times 9–9.5 cm, 2 to 2.2 times longer than wide, 1.2 to 1.3 times longer than posterior lobes, broadest below middle, usually near base, \pm symmetrical; posterior lobes directed outward, 13.5–17.5 \times 4–5.5 cm, 3.4 to 3.8 times longer than wide, narrowly rounded to bluntly acute at apex, broadest below middle, \pm symmetrical to weakly inequilateral, the inner side occasionally weakly narrower, \pm rounded toward base, briefly attenuate and decurrent onto petiole; outer side \pm straight toward base; all venation (except reticulate) drying weakly to moderately darker than surface; midrib round-raised on lower surface, drying \pm raised; **basal veins** 4 to 6 pairs, coalesced into prominent posterior rib; primary lateral veins 3 to 4 pairs, arising at 30°–60°, most acutely toward apex, weakly to moderately arcuate, occasionally strongly arcuate or irregularly ascending, convex on lower surface, drying \pm flattened to weakly raised; secondary veins raised on lower surface, drying \pm flattened to weakly raised; tertiary veins drying entirely or in part prominulous and otherwise distinct on lower surface; reticulate veins drying obscure; collective veins 3, the innermost arising from one of the lowermost lateral veins on inner side of posterior lobe, loop-connected with all preceding lateral veins, parallel to margin or moderately scalloped, 3–7 mm from margin. INFLORESCENCES erect, to 3 per axil; peduncle held within the sheath, 11–15 cm \times 1.5–3.5 mm, drying weakly glossy

to semiglossy, dark brown; **spathe** erect, cream-colored or yellow, 7–8.5 cm long, acuminate at apex; spathe tube 3.2–4.4 cm \times 3–4 mm, drying matte, dark reddish brown on outer surface, weakly glossy on inner surface; spathe blade 4–4.5 cm \times 5–6 mm, drying weakly glossy to semiglossy, pale-medium to medium-dark reddish brown on both surfaces, marcescent, erect after anthesis; **spadix** erect, 6–8 cm long, sessile, adnate to spathe 2.7–3.8 cm at base, the entire length of pistillate portion and occasionally narrowly onto sterile staminate portion; pistillate portion 2.7–3.8 cm \times 2–3 mm, wider than thick, drying cream to tan; fertile staminate portion cream or yellow, 2.5–3.5 cm \times 3–4 mm, \pm cylindrical, narrowly rounded at apex, drying medium to medium-dark yellowish brown; sterile staminate portion 3–8 \times 2–3 mm, cylindrical or weakly broadest at apex, drying medium to medium-dark yellowish brown, minutely darker red-brown-speckled; pistils weakly coherent to laxly arranged, ca. 3 across the axis (viewed from above), ca. 1.5 mm long; ovaries subglobose, ca. 1 \times 1.5–2 mm, drying dark brown; style Type 10 (Fig. 1), ca. 0.5 \times 1–1.5 mm (attenuate portion ca. 0.4 mm long), comprising 1/4 to 1/3 of the length of pistil, as broad as to weakly narrower than ovary apex, the margins weakly or not at all coherent with those of adjacent styles; **stigma** ca. 0.5 mm diam., weakly elevated on and weakly broader than narrowed portion of style, drying yellowish tan; synandria 1–1.3 \times 1.8–2 mm, coherent, truncate, (2)3- to 4(5)-lobed, (2)3- to 4(5)- (mostly 4); sterile flowers 0.5–1 mm long, 1 \times 2 mm diam. and elongated in direction of axis, coherent, truncate, irregularly subprismatic, in 3 to 5 whorls. Berries not known.

Phenology. Flowering is only known to occur in *Chlorospatha nicolsonii* during the months of January and February.

Discussion. *Chlorospatha nicolsonii* is known only from the Parque Nacional Natural Las Orquídeas on the western slopes of the Cordillera Occidental in Antioquia Department, Colombia, at 1500–1800 m elevation. The park area exhibits a high level of endemism in *Chlorospatha*. The species occurs in premontane wet forest, possibly also in tropical wet forest.

Chlorospatha nicolsonii is a member of *Chlorospatha* sect. *Occidentales* and is distinguished by its subhastate, triangular leaf blades with narrow posterior lobes nearly as long as the anterior lobe. The posterior rib is not naked, the inner margins of the posterior lobes being decurrent onto the petiole. The species is also characterized by its petiole, which is sheathed only one third of its length, short peduncle (11–15 cm long), entirely yellow or

cream-colored, and cream or yellow synandria. The spadix is adnate to the spathe the entire length of the pistillate portion and onto half or the entire length of the sterile staminate portion. The species has relatively long internodes, 2–4 cm, and is occasionally hemiepiphytic.

Chlorospatha nicolsonii would be most easily confused with *C. tokioensis* from Valle Department, at Estación Microndas Tokio near Queremal, on the western slopes at 2000–2100 m elevation. Both species have the petiole sheathed one third of its length, subhastate leaf blades with long, narrow posterior lobes, and short peduncles. *Chlorospatha nicolsonii* is occasionally hemiepiphytic, with longer internodes, 2–4 cm long versus 1–1.5 cm long in *C. tokioensis*, which is consistently terrestrial. The leaf blades of *C. tokioensis* have five to six pairs of primary lateral veins and dry green, with the anterior lobe narrower and longer relative to the length of the posterior lobes. The leaf blades of *C. nicolsonii* have three to four pairs of primary lateral veins and dry brown to greenish brown, with the anterior lobe broad, and the inner margin of the posterior lobe decurrent onto the petiole. The posterior lobe is decurrent onto the posterior rib, which is naked 3–12 mm on each side in *C. tokioensis*. Pale raphid cells are visible on the upper blade surface in the latter species, but do not occur on the blades of *C. nicolsonii*. *Chlorospatha tokioensis* has a larger inflorescence, with the spathe 8.8–9.5 cm long, the tube green, the blade white, and the sterile staminate portion of the spadix uncommonly short, less than 2 mm long, with the sterile flowers laxly arranged and fungiform or deeply lobed. *Chlorospatha nicolsonii* differs in having the spathe 7–8.5 cm long, entirely yellow or cream-colored, and the sterile staminate portion of the spadix 3–8 mm long, with the flowers subprismatic and densely arranged. The style of the latter species is only as broad as the ovary apex and very briefly attenuated, whereas that of *C. tokioensis* is broader than the ovary apex and long-attenuated.

Chlorospatha nicolsonii could possibly be confused with *C. noramurphyae* from Valle Department, in the vicinity of Cali on the eastern slopes of the Cordillera Occidental at 1700 m elevation. Both species have subhastate leaf blades with long, narrow posterior lobes, but in *C. noramurphyae*, the posterior rib is naked and there are five to seven pairs of primary lateral veins versus three or four pairs in *C. nicolsonii* in which the posterior rib is not naked. The latter species further differs in having the petiole sheathed one third of its length, the peduncle short (11–15 cm long), and the inflorescence smaller, to 8.5 cm long. The petiole of *C. noramurphyae* is sheathed three

fourths of its length; the peduncle is 32 cm long; and the inflorescence is 12.5 cm long. The spathe is red in the latter species, and the sterile staminate portion of the spadix is 1.8–2.5 cm long, with the flowers branched and laxly arranged, thus differing from *C. nicolsonii* in which the spathe is entirely cream or yellow and the sterile staminate portion is less than 1 cm long, with the flowers densely arranged and subprismatic. The style of *C. nicolsonii* is briefly attenuated, whereas that of *C. noramurphyae* is long-attenuated.

Additional specimen examined. COLOMBIA. **Antioquia:** Parque Nac. Nat. Las Orquídeas, Calles–Venados rd., 1500 m, *Cogollo et al.* 3976 (JAUM-016944).

52. *Chlorospatha noramurphyae* Croat & L. P. Hannon, sp. nov. TYPE: Colombia. Valle: Cali, Villa Carmelo, 1700 m, 15 May 1982, *H. Murphy* 383 (holotype, MO-3046149!; isotype, COL-259232!). Figure 39D.

Herba minus quam 1 m. Petiolus 36–41 cm longus, vaginatus per usque ad 30 cm; lamina foliaris subhastata, 29–35 × 23–28 cm, lobis posterioribus 16–16.5 × 5.5–6 cm, nervis basalibus utroque 5 ad 7, nervis primariis lateralibus utroque 5 ad 7. Inflorescentia 1 in quaque axilla; pedunculus ca. 32 cm × 2–4 mm; spatha rubra, ca. 12.5 cm longa, tubo 5.5–6 mm diam., lamina complanata ca. 6 cm × 9 mm; spadix ca. 10.5 cm longus.

Terrestrial herb, less than 1 m tall; stem, internodes, and cataphylls not known (all measurements made from dried material). LEAVES 1 to 2; **petioles** 36–41 cm long, drying glabrous, matte to weakly glossy, medium-dark to dark or blackish brown, sheathed to 30 cm, ca. 3/4 of total length; sheath decurrent at apex; free portion 2.5–3 mm diam. midway; **blades** subhastate, 29–35 × 23–28 cm, 1 to 1.5 times longer than wide, acuminate at apex, broadest at base, 2 to 2.5 times wider at base than across anterior lobe (measured tip to tip across posterior lobes), occasionally weakly constricted in area of petiole attachment, drying thinly coriaceous, moderately bicolorous; upper surface drying matte, dark brown; lower surface drying weakly glossy to semiglossy, olive-brown; anterior lobe 21–22 × 11–11.5 cm, 1.9 times longer than wide, 1.3 to 1.4 times longer than posterior lobes, broadest below middle, ± symmetrical; posterior lobes directed outward, 16–16.5 × 5.5–6 cm, 2.6 to 3.2 times longer than wide, bluntly acute to narrowly rounded at apex, broadest below middle, ± symmetrical, the inner side weakly to broadly rounded toward base and briefly attenuate onto posterior rib; outer side straight to weakly concave toward base; midrib narrowly raised on lower surface, drying ± flattened, weakly paler to weakly

darker than surface; **basal veins** 5 to 7 pairs, coalesced into a prominent posterior rib; posterior rib naked ca. 1 cm per side; primary lateral veins 5 to 7 pairs, arising at 50°–60°, weakly arcuate, occasionally straight, convex on lower surface, drying entirely \pm flattened or in part weakly raised toward base, concolorous to weakly darker than surface; secondary veins drying weakly raised on lower surface, \pm concolorous to weakly darker than surface; tertiary veins drying distinct on lower surface, in part weakly prominulous, otherwise flat, \pm concolorous to weakly darker than surface; reticulate veins drying in part visible on lower surface; collective veins 3, the innermost arising from one of the lowermost lateral veins on inner side of posterior lobe, loop-connected with all preceding lateral veins, parallel to and 4–6 mm from margin. INFLORESCENCE erect, 1 per axil; peduncle held within the sheath, ca. 32 cm \times 2–4 mm, drying weakly glossy, medium-dark to dark brown; **spathe** red, weakly cucullate, ca. 12.5 cm long, apex not known; spathe tube 6.5–7 cm \times 5.5–6 mm, drying matte, dark brown on outer surface, weakly glossy, reddish brown on inner surface; spathe blade ca. 6 cm long, 9 mm wide (flattened), drying matte, medium-dark tan; **spadix** curved forward, ca. 10.5 cm long (est.), sessile, adnate to spathe 5.2–5.5 cm at base, the entire length of pistillate portion, occasionally onto sterile staminate portion 2–3 mm; pistillate portion 5.2–5.5 cm \times ca. 3 mm, drying medium-dark to dark reddish brown; fertile staminate portion pink, total length not known, 2–3 mm diam., narrowed toward base, drying pale grayish brown; sterile staminate portion 1.8–2.5 cm \times 1.5–3 mm, drying dark reddish brown; pistils weakly coherent, ca. 4 across the axis (viewed from above), 2–2.5 mm long; ovaries subglobose, 2.5–3 mm diam., drying cream to brownish cream, with or without moderately darker veins; style Type 8 (Fig. 1), 0.8–1 \times 1.5–2.2 mm, comprising ca. 1/2 of the length of pistil, broader than ovary apex, the margins not coherent with those of adjacent styles; **stigma** ca. 0.2 mm diam., elevated on and wider than narrowed portion of style, drying yellowish to amber; synandria ca. 1 \times 1–1.2 mm, coherent, truncate, deeply 3- to 4-lobed, 3- to 4-androus; sterile flowers 0.5–0.8 \times ca. 1 mm, mostly 1-branched and subrounded in basal 10 whorls (some 2- to 3-branched), markedly laxly arranged, most conspicuously so toward base (axis mostly bare and few flowered), the branches convex at apex, abruptly narrowed below, otherwise 0.2–0.5 mm diam. and deeply irregularly lobed in apical 1 to 2 whorls, in 12 or more whorls. Berries not known.

Phenology. Flowering is only known to occur in *Chlorospatha noramurphyae* during the month of May.

Etymology. The epithet is named for Honora Murphy, formerly of Duke University and the Missouri Botanical Garden, former assistant of the senior author and the collector of the type of *Chlorospatha noramurphyae*.

Discussion. *Chlorospatha noramurphyae* is known only from the type collection made in Valle Department, Colombia, in the vicinity of Calí, near Villa Carmelo, in premontane wet forest on the eastern slopes of the Cordillera Occidental at 1700 m elevation. The species would be expected to occur elsewhere in the department, possibly also on the western slopes. When the collection was made, the type locality was in primary forest surrounded by coffee farms and was being rapidly cut. It is likely that the only known population has been destroyed. The species was found growing on steep slopes in red clay soil subsumed by shale, with a thick layer of humus. The label notes report 1000 mm of annual rainfall for the area.

Chlorospatha noramurphyae is a member of *Chlorospatha* sect. *Occidentales* and is distinguished by its petiole, which is sheathed ca. three fourths of its length, and subhastate leaf blades, with the posterior lobes narrow and long relative to the length of the anterior lobe. The species is also distinguished by its long, weakly cucullate, red spathe (ca. 12.5 cm long) and its spadix, with the fertile staminate portion pink and the sterile staminate portion unusually long, 1.8–2.5 cm long. The sterile flowers are noteworthy, being in ca. 12 whorls, with most 1-branched and laxly arranged, and the axis almost bare in the basal one third of the sterile staminate portion.

Chlorospatha noramurphyae could be easily confused with *C. giraldoi*, also from Valle, near Calí, on the eastern and western slopes of the Cordillera Occidental, and is possibly sympatric with that species (see discussion under *C. giraldoi*).

Chlorospatha noramurphyae could possibly be confused with *C. ricaurtensis* from Reserva La Planada on the western slopes of the Cordillera Occidental in Nariño Department, Colombia, at 1800 m elevation. *Chlorospatha ricaurtensis* has sagittate leaf blades that dry semiglossy on both surfaces, with three pairs of primary lateral veins, and the posterior lobes directed toward the base. *Chlorospatha noramurphyae* differs in having subhastate leaf blades that dry matte on the upper surface and weakly glossy on the lower surface, with five to seven pairs of primary lateral veins. The spathe of the latter species is entirely red, differing from that of *C. ricaurtensis*, which has a purple tube and weakly purple-tinged, greenish cream blade. The pistils of *C. ricaurtensis* are densely arranged, with the style

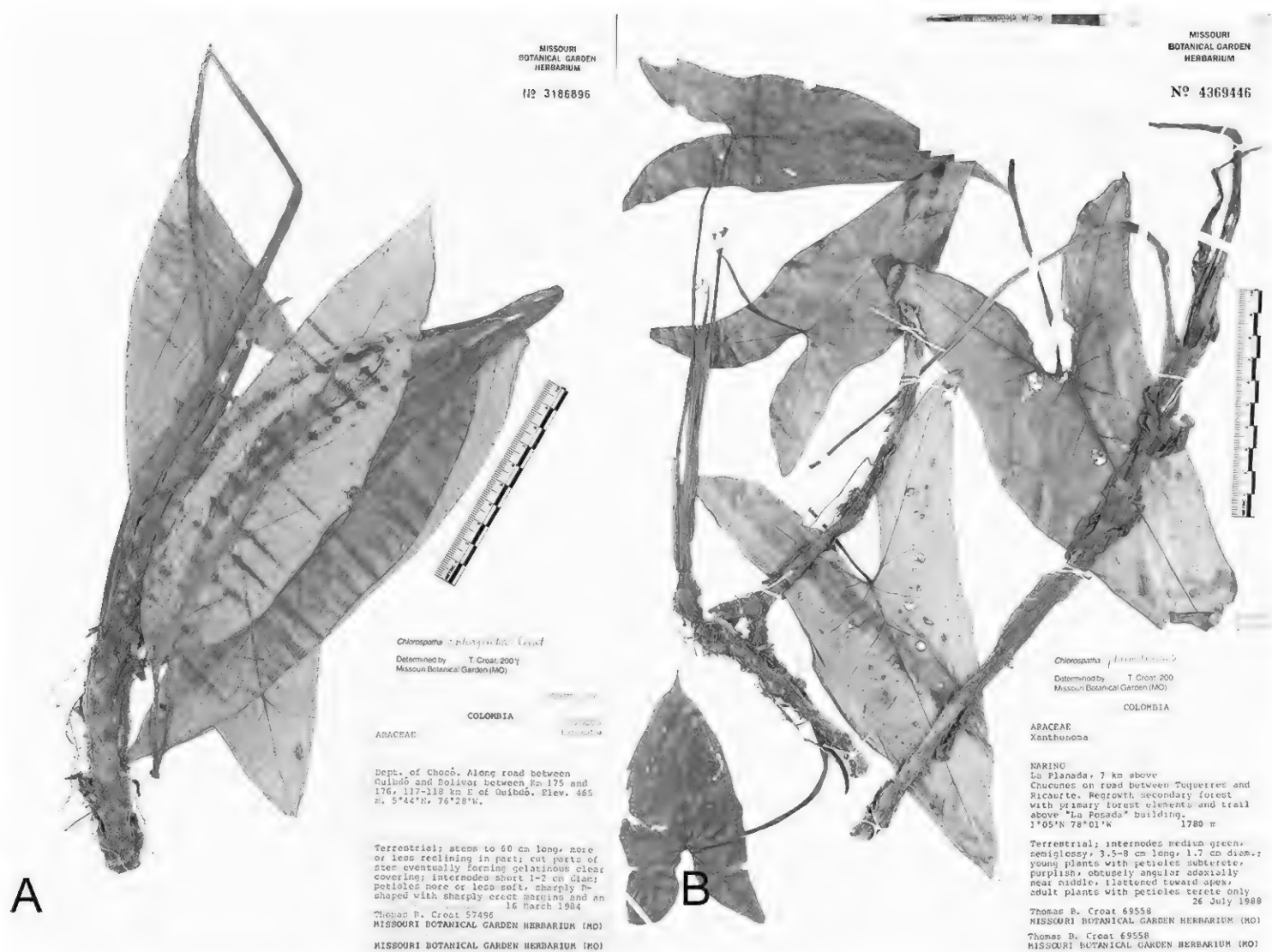


Figure 40. —A. *Chlorospatha oblongifolia* Croat & L. P. Hannon, the paratype specimen Croat 57496 (MO-3186896). —B. *Chlorospatha planadensis* Croat & L. P. Hannon, the paratype specimen Croat 69588 (MO-4369446).

(Type 9, Fig. 1) comprising ca. one third of the length of the pistil, whereas those of *C. noramurphyae* are laxly arranged, with the style (Type 8, Fig. 1) comprising one half of the length of the pistil. The synandria of *C. ricourtensis* are 5- to 6-androus, a rare condition in the genus, thus differing from those of *C. noramurphyae*, which are 3- to 4-androus. In *C. noramurphyae*, the sterile staminate portion of the spadix is longer, 1.8–2.5 cm long, although the spadix is shorter than that of *C. ricourtensis* in which the sterile portion is 1.5–1.8 cm long. The sterile flowers are similar in both species, but are laxly arranged in *C. noramurphyae* and densely arranged in *C. ricourtensis*.

53. *Chlorospatha oblongifolia* Croat & L. P. Hannon, sp. nov. TYPE: Colombia. Chocó: vic. El Viente, 410 m, 5°45'N, 76°30'W, 16 Aug. 1997, Croat & J. Gaskin 80957 (holotype, MO-5796074!; isotypes, F!, HUA!, K!, NY!, US!). Figures 3A–F, 40A.

Herba ca. 50 cm; internodia ca. 1 × 0.8–2 cm; cataphylla 9–18 cm longa. Petiolus (12–)14.5–34 cm longus, vaginatus per 6–10.5 cm; lamina foliaris oblonga vel ovato-elliptica, (15–)18–33 × (2.7–)3.5–13.5 cm, nervis primariis later-

alibus utroque (6)7–10. Inflorescentiae 6 in quaque axilla; pedunculus 5–6 cm × 3–4 mm; spatha erecta, 3–5.3 cm longa, tubo 3–6 mm diam.; spadix erectus, 2.2–3.9 cm longus.

Terrestrial herb, ca. 50 cm tall; stem decumbent, to 60 cm long, erect, ca. 15 cm, with remnants of old leaf bases and cataphylls persisting ± intact or semi-intact along its length, eventually ± fibrous; sap ± transparent, becoming gelatinous; internodes ca. 1 × 0.8–2 cm, semiglossy, dark green, quickly becoming gray-green, drying weakly glossy, medium to dark brownish gray; cataphylls 9–18 cm long, obtuse with acumen at apex, obtusely 1-ribbed toward apex or entirely acutely 2-ribbed, thin, semiglossy, pale-medium green, drying weakly glossy to semiglossy, medium-dark reddish brown. LEAVES 3 to 4, erect-spreading; **petioles** (12–)14.5–34 cm long, moderately firm or soft, glabrous, weakly glossy, medium to dark green, drying weakly glossy to semiglossy, dark reddish brown, sheathed 6–10.5 cm, ca. 1/4 to 1/3 of total length; sheath decurrent at apex; free portion 4–8 mm diam. midway, frequently thicker than broad, obtusely 1-ribbed medially, sharply D- or C-shaped, the margins bluntly acute, frequently becoming acute and alate toward apex (to 1.5 mm wide near apex); **blades** oblong to ovate-elliptic, (15–)18–33 × (2.7–)

3.5–13.5 cm, briefly narrowly acuminate at apex, (2.4 to) 3.5 to 5.6 times longer than wide, broadest at or below middle, \pm acute at base and usually inequilateral at point of attachment, occasionally weakly cordulate, decurrent onto petiole, \pm symmetrical, thin to thinly coriaceous, weakly to conspicuously bicolorous; upper surface quilted, semiglossy to glossy, medium-dark to dark green, drying weakly glossy to semiglossy, dark yellowish brown; lower surface weakly glossy to semiglossy, drying semiglossy to glossy, weakly to moderately paler; midrib deeply sunken on upper surface, round-raised on lower surface, weakly paler than surface, drying \pm flattened, moderately darker than surface; primary lateral veins (6) 7 to 10 pairs, arising at 27° – 40° (– 45°), \pm straight to weakly arcuate, occasionally moderately arcuate, quilted-sunken on upper surface, convex on lower surface, concolorous, drying flattened, weakly to moderately darker than surface; secondary veins sunken on upper surface, raised on lower surface, drying weakly raised, concolorous to weakly darker than surface; tertiary veins entirely raised or in part raised and otherwise prominulous on lower surface, drying in part weakly prominulous, otherwise flat, concolorous to weakly darker than surface; reticulate veins obscure, drying obscure; collective veins 3, the innermost arising from the base, loop-connected with all preceding lateral veins, \pm parallel to and 3–8 mm from margin. INFLORESCENCES erect, to 6 per axil, emitting a spicy-sweet fragrance at anthesis; peduncle held within the sheath, 5–6 cm \times 3–4 mm, weakly broader than thick, obtusely triangular and flattened adaxially, weakly sulcate at apex, weakly glossy, pale to pale-medium green, drying weakly glossy, dark reddish brown; **spathe** erect, 3–5.3 cm long, ovate, cuspidate at apex; spathe tube matte, white to pale green on outer surface, weakly glossy to semiglossy on inner surface, 1.2–2.3 cm \times 3–6 mm, weakly thicker than broad, drying matte, medium-dark reddish brown on outer surface, matte to weakly glossy on inner surface; spathe blade weakly glossy, white to greenish cream on outer surface, semiglossy on inner surface, 1.8–3 cm \times 3–5 mm, drying weakly glossy, pale-medium reddish brown on both surfaces, opening broadly at anthesis, marcescent, erect after anthesis; **spadix** erect, 2.2–3.9 cm long, sessile, adnate to spathe 5–9 mm at base, ca. 1/2 to 3/4 of the length of pistillate portion; pistillate portion greenish cream to pale green, 0.7–1.5 cm \times 2–4 mm, broadest midway, drying dark reddish brown; fertile staminate portion white to weakly green-tinged cream, 1.1–1.9 cm \times 2–4 mm, weakly cylindroid, thicker than broad, \pm clavate, bluntly acute at apex, drying medium

yellowish brown; sterile staminate portion white or cream, 3–10 \times 1.5–3 mm, broadest at base, drying medium to medium-dark yellowish brown; pistils weakly coherent, ca. 3 to 4 across the axis (viewed from above), 1.2–1.5 mm long; ovaries \pm cylindrical, greenish cream to pale green, ca. 1 \times 1–1.8 mm, drying pale tan, 3-locular, with axile placentation; ovules 8 to 10 per locule, anatropous, 2- to 3-seriate; funicle longer than ovule; style Type 10 (Fig. 1), 0.3–0.5 \times 0.7–1.2 mm (attenuate portion ca. 0.3 mm long), comprising 1/4 to 1/3 of the length of pistil, narrower to weakly broader than ovary apex, with red chromoplasts, the margins not coherent with those of adjacent styles; **stigma** greenish cream, ca. 0.2–0.25 mm diam., weakly elevated on narrowed portion of style, drying medium to dark reddish brown; synandria 1–1.1 \times 1.5–1.7 mm, coherent, truncate, 2- to 3-lobed, 2- to 3-androus (mostly 3); pollen exine smooth (Fig. 3A–F); sterile flowers 0.5–0.7 \times 1.2–2 mm, weakly elongated in direction of axis, \pm coherent, truncate, subprismatic or prismatic (in apical 1 to 3 whorls), in 3 to 7 whorls. Berries not known.

Phenology. Flowering is only known to occur in *Chlorospatha oblongifolia* in the months of March, April, and July through November. Inflorescences are fragrant and emerge in slow progression, with several days between anthesis of one inflorescence and emergence of the next inflorescence at the apex of the petiole sheath.

Etymology. The epithet is taken from the Latin “oblongus,” meaning “oblong,” referring to the unusual leaf blade shape of *Chlorospatha oblongifolia*.

Discussion. *Chlorospatha oblongifolia* is known from a relatively small area to the east of Quibdó, just east of Tutunendo in Chocó Department, Colombia, in tropical rainforest at 410–465 m elevation on the western slopes of the Cordillera Occidental. The species would be expected to occur elsewhere within the department.

Chlorospatha oblongifolia is a member of *Chlorospatha* sect. *Occidentales* and is distinguished by its semiglossy to glossy, dark green, narrowly oblong to ovate-elliptic leaf blades that are much longer than wide, more or less acute at the base and usually inequilateral at the point of petiole attachment. This mature blade shape is found in only one other species, *C. portillae*, and only rarely in juvenile specimens of a few additional species. The species is also distinguished by its petiole, which is sheathed one fourth to one third of its length, with the free portion obtusely 1-ribbed medially and sharply D- or

C-shaped, with the margins bluntly acute midway, becoming acute and occasionally alate near the apex, with the alate portion to 1.5 mm wide. The peduncle is unusually thick for its length (5–6 cm long), being ca. 4 mm diameter. Such large diameter is usually observed only in much larger species with long peduncles. The inflorescence is also unusually small, 3–5.3 cm long. The style is narrowly attenuated, thus elevating the stigma.

Chlorospatha oblongifolia could not be confused with any known species of *Chlorospatha*. Vegetatively, it most closely resembles *C. portillae*, which occurs only on the eastern slopes of the Andes in Zamora-Chinchipe Province in southeastern Ecuador. *Chlorospatha oblongifolia* has petioles that are sharply C- or D-shaped, with raised or alate margins and a medial rib, whereas the petiole of *C. portillae* is terete and lacks a medial rib. Both species have relatively short peduncles and small inflorescences, but *C. oblongifolia* differs in having no more than six inflorescences in a sympodium, with the peduncle held within the petiole sheath and the spathe entirely green. The peduncle and spathe are purple or purplish in *C. portillae*, which has 10 inflorescences per sympodium, with the sympodium held within a sympodial cataphyll. The most notable differences are in the pistils. The style of *C. portillae* lacks a mantle, whereas that of *C. oblongifolia* is expanded into a prominent mantle.

Paratype. COLOMBIA. **Chocó:** along Quibdó–Bolívar rd., betw. Km. 175 & Km. 176, 117–118 km E of Quibdó, 465 m, 5°44'N, 76°28'W, 16 Mar. 1984, Croat 57496 (CHOCO, COL, HUA, JAUM, MO-3186896, MO [2]-3186897).

54. *Chlorospatha planadensis* Croat & L. P. Hannon, *Aroideana* 33: 81–84. 2010. TYPE: Colombia. Nariño: Res. Nat. La Planada, 7 km from Chucunés, 1800 m, 1°10'N, 77°58'W, 1 Nov. 1987, O. Benavides 8686 (holotype, MO-3656423; isotype, PSO not seen). Figure 40B.

Terrestrial or hemiepiphytic herb, to ca. 1 m tall; stem decumbent, with remnants of old cataphylls persisting \pm intact along its length; sap milky; internodes (2–)3.5–8 \times 1.7 cm, semiglossy, medium green, occasionally weakly violet-tinged, drying matte to weakly glossy, dark green to blackish green (all measurements made from dried material); cataphylls 10–33 cm long, obtuse with subapical apiculum at apex, 1-ribbed abaxially, drying weakly glossy to semiglossy, medium-dark reddish brown. LEAVES 1 to 3, erect-spreading; **petioles** 66–77 cm long, glabrous, green, drying weakly glossy to semiglossy, dark brown, sheathed 28–29 cm, slightly more than

1/3 of total length; sheath decurrent at apex; free portion 4–7 mm diam. midway, terete, obtusely angular at apex; **blades** subhastate, broadly triangular, 31–33.5 \times 23–27 cm, 1.2 to 1.3 times longer than wide, weakly acuminate at apex, broadest at base, ca. 1.5 times wider at base than across anterior lobe (measured tip to tip across posterior lobes), thinly coriaceous, moderately to prominently bicolorous; upper surface broadly quilted, semiglossy, dark green, drying weakly glossy to semiglossy, brownish green; lower surface semiglossy, drying semiglossy to glossy, weakly to moderately paler; anterior lobe 21–23 \times 17.5–18 cm, 1.2 to 1.3 times longer than wide, 1.4 to 1.6 times longer than posterior lobes, broadest at or near base, \pm symmetrical to weakly inequilateral, occasionally with one side ca. 1 cm wider than opposite side; posterior lobes directed somewhat outward, 14–16 \times 8.5–10 cm, 1.4 to 1.7 times longer than wide, narrowly rounded at apex, broadest at base, weakly inequilateral, the inner side narrower, weakly to broadly rounded toward base, moderately attenuate and decurrent onto petiole or possibly occasionally onto posterior rib; outer side 1.3 to 1.4 times wider than inner side midway, \pm straight to weakly concave or weakly convex toward base; midrib and major venation deeply sunken on upper surface, round-raised on lower surface, drying weakly raised to weakly flattened, weakly darker than surface; **basal veins** 5 pairs, coalesced into a prominent posterior rib; primary lateral veins 5 pairs, arising at 40°–60°, most acutely toward apex, weakly to moderately arcuate; secondary veins sunken on upper surface, raised on lower surface, drying weakly raised, weakly darker than surface; tertiary veins in part sunken on upper surface, raised on lower surface, darker than surface, drying weakly prominulous, weakly darker than surface; reticulate veins visible, flat on lower surface, darker than surface, drying in part visible, distinct, \pm concolorous; collective veins 3, the innermost arising from one of the lateral veins on inner side of posterior lobe, loop-connected with all preceding lateral veins, weakly scalloped, usually moderately remote from margin, 5–12 mm from margin. INFLORESCENCE erect, 1 per axil; peduncle held within the sheath, 49 cm \times 3–5 mm, drying semiglossy, dark reddish brown; **spathe** length not known; spathe tube dark violet or purple, ca. 5.2 cm \times ca. 5 mm, drying matte to weakly glossy, dark reddish brown on both surfaces; spathe blade not known, possibly dark purple; **spadix** total length not known, sessile, adnate to spathe ca. 4 cm at base, the entire length of pistillate portion; pistillate portion ca. 4 cm \times ca. 5 mm, drying dark reddish brown; fertile staminate portion cream-colored or white, length not

known, 2–4 mm diam., narrowed at base, drying dark reddish brown; sterile staminate portion ca. 1 cm \times 2.5–3.5 mm, broadest near apex, drying medium-dark to dark reddish brown; pistils weakly coherent, ca. 4 across the axis (viewed from above), ca. 2 mm long; ovaries subglobose, ca. 1 \times ca. 2–2.2 mm; style Type 5 (Fig. 1), ca. 0.8–1 \times 2 mm, comprising ca. 1/2 of the length of pistil, much broader than ovary apex, the margins \pm coherent with those of adjacent styles; **stigma** ca. 0.3–0.8 mm diam., prominent, elevated on and broader than narrowed portion of style, drying dark reddish brown, occasionally paler; synandria 1–1.3 \times 1.5 mm, or 2 \times 1 mm diam. and \pm elongated in direction of axis, coherent, truncate, 3- to 4-lobed, 3- to 4-androus; sterile flowers ca. 1 \times ca. 1 mm in basal whorl, otherwise 1.5–2 \times 3 mm diam. and elongated in direction of axis, coherent, truncate, subprismatic, in 3 to 5 whorls. Berries not known. JUVENILE plants with internodes 1.5–3 \times ca. 1 cm; petioles 17–22 cm long, purplish, sheathed ca. 1/3 of total length; free portion subterete, obtusely angular midway, flattened toward apex; blades sagittate, narrowly triangular, 16–21.5 \times 8–13 cm, frequently weakly to moderately constricted in area of petiole attachment, drying moderately bicolorous.

Phenology. Flowering is only known to occur in *Chlorospatha planadensis* during the months of January and November.

Discussion. *Chlorospatha planadensis* is known only from the western slopes of the Cordillera Occidental, at La Planada Reserve in Nariño Department in southern Colombia, at 1780–1800 m elevation. The area is north of Ricaurte, near Chucunés, in an area of regrowth secondary forest that includes primary forest elements. The species was collected in premontane wet forest, possibly also in an area of either premontane wet forest or lower montane wet forest, and would be expected to occur elsewhere in the department and southward into northern Ecuador.

Chlorospatha planadensis is a member of *Chlorospatha* sect. *Occidentales* and is distinguished by its terrestrial or hemiepiphytic habit and markedly long internodes, the longest in the genus, which are semiglossy, medium green, and occasionally violet-tinged. The species is also distinguished by its semiglossy, dark green, subhastate, and broadly triangular leaf blades with broad posterior lobes. *Chlorospatha planadensis* is unusual in the genus in having the petiole sheathed only one third of its length, but with the peduncle much longer than the sheath. The peduncle is usually only slightly longer or shorter than the petiole sheath in *Chlorospatha*.

The inflorescence of *C. planadensis* is presumably large, the spathe tube being 5.2 cm long and dark violet to purple on both surfaces. The spathe blade was not examined, but label notes indicate that it too is possibly dark purple.

Chlorospatha planadensis could be most easily confused with *C. ricaurtensis*, with which it is sympatric at La Planada Reserve. Both species have semiglossy leaf blades, semiglossy, medium green internodes, and purple spathe tubes. *Chlorospatha ricaurtensis* is terrestrial, having been collected in a pasture, with short internodes and sagittate leaf blades with three pairs of primary lateral veins and narrow posterior lobes. *Chlorospatha planadensis* differs in being frequently hemiepiphytic and having long internodes, subhastate blades with five pairs of primary lateral veins, and broad posterior lobes. The petiole of *C. ricaurtensis* is sheathed two thirds of its length, with the sheath free-ending at the apex, and the peduncle is 23–31 cm long. In *C. planadensis*, the petiole is sheathed one third of its length, with the sheath decurrent, and the peduncle is much longer, 49 cm long. The inflorescence of *C. planadensis* is probably significantly smaller, with the tube 5.2 cm long versus 6.5–7 cm long in *C. ricaurtensis*. The sterile staminate portion of the spadix of *C. ricaurtensis* is unusually long (1.5–1.8 cm), with most flowers branched, whereas that portion is short in *C. planadensis* (1 cm long), with the flowers subprismatic. The style of *C. ricaurtensis* (Type 9, Fig. 1) comprises ca. one third of the length of the pistil, whereas that of *C. planadensis* (Type 5, Fig. 1) comprises ca. one half of the length. The synandria of *C. ricaurtensis* are 5- or 6-androus, a rare condition in the genus, whereas those of *C. planadensis* are 3- or 4-androus.

Only the type specimen is fertile, with only a partial inflorescence available for examination. *O. Benavides 11253* is a sterile collection, but the label notes indicate that the spathe is purple and the spadix white; therefore, it would appear to accord with this species, in most respects.

Additional specimens examined. COLOMBIA. **Nariño:** La Planada Reserve, 1°10'N, 77°58'W, 17 Jan. 1990, *O. Benavides 11253* (MO, PSO); La Planada Res., 7 km above Chucunés on Túquerres–Ricaurte rd., trail above La Posada bldg., 1780 m, 1°05'N, 78°01'W, 26 July 1988, *Croat 69558* (B, K, MO-4369446, US); Res. Nat. La Planada, Mpio. Ricaurte, Border Píalapi, 1800 m, 12 Nov. 1993, *C. Restrepo CR 667* (MO).

55. *Chlorospatha plowmanii* (Madison) Croat & L. P. Hannon, comb. nov. Basionym: *Caladium plowmanii* Madison, Phytologia 35: 104. 1976. TYPE: Ecuador. Sucumbíos: 31 mi. W of Lago

Agrio on rd. to Baeza, 700 m, *T. Plowman*, *C. Sheviak* & *E. W. Davis* 3979 (holotype, GH!; isotypes, M!, MO!, P not seen, SEL!). Figures 3G–L, 41A–D.

Terrestrial herb, 30–50 cm tall, in small colonies; stem decumbent, with remnants of old cataphylls persisting as a few short, brown fibers, occasionally in part semi-intact, occasionally producing bulbils randomly along its length; bulbils solitary, $1\text{--}3 \times 1\text{--}3$ mm, subglobose; sap milky; internodes $1\text{--}3 \times 0.8\text{--}1.5$ cm, semiglossy, medium to dark green, becoming matte to weakly glossy with age, drying matte, dark brown or greenish brown; cataphylls 6–11 cm long, obtuse and inequilateral with acumen at apex (acumen 0.5–1.5 cm long), obtusely 1(2)-ribbed abaxially, matte to weakly glossy, pale to medium green, rarely purple-mottled in narrow transverse bands (*Croat et al.* 88008A), drying matte, medium to dark brown. LEAVES 5 to 10, erect, erect-spreading, spreading and reflexed-spreading; **petioles** 13–26 cm long, glabrous, matte, medium to medium-dark green, rarely dark purple (*Croat et al.* 96410), drying matte, medium to dark brown or greenish brown, sheathed 4–7.5 cm, ca. 1/4 of total length, occasionally 1/3, rarely 1/2 (in Zamora-Chinchipe); sheath decurrent at apex, or frequently with one side wider and free-ending, the sides \pm erect; free portion 2.5–4 mm diam. midway (drying 2–3.5 mm diam.), terete or subterete, obtusely to weakly acutely sulcate in apical 5 cm, rarely sharply D-shaped and obtusely sulcate throughout (*Croat et al.* 88008A); **blades** held \pm horizontally, hastate to subhastate, occasionally subsagittate (in young blades), $12.5\text{--}25 \times 12.5\text{--}21$ cm, 1 to 1.3(to 1.5) times longer than wide, acute to acuminate or apiculate at apex, frequently as wide as long, broadest at base, (1.5 to) 1.7 to 2.8 times wider at base than across anterior lobe (measured tip to tip across posterior lobes), occasionally weakly constricted in area of petiole attachment, thin, moderately bicolorous, the margins frequently narrowly undulate; upper surface broadly quilted, velvety, dark green to yellowish green, drying matte to velvety-matte or weakly glossy, dark green; lower surface reticulate, weakly glossy, narrowly colliculate along all venation, drying weakly glossy to semiglossy, weakly to moderately paler; anterior lobe $11\text{--}20 \times 6.5\text{--}10.5$ cm, 1.4 to 2 times longer than wide, 1.5 to 2 times longer than posterior lobes, broadest at or near base; posterior lobes directed prominently outward, (5.5–) $6.5\text{--}12.5 \times (2\text{--})2.8\text{--}5.5$ cm, 1.9 to 3.6 times longer than wide, acute to bluntly acute at apex, rarely narrowly rounded, broadest at base or below middle, symmetrical or moderately inequilateral, the inner side narrower, weakly to broadly rounded toward base,

briefly to moderately attenuate onto posterior rib; outer side 1.3 to 1.5 times wider than inner side midway, weakly concave or occasionally weakly convex toward base; midrib and major venation deeply sunken on upper surface, round-raised on lower surface, green and weakly darker than surface, rarely moderately purple-tinged, drying raised, weakly to prominently darker than surface; **basal veins** 2 to 3 pairs, coalesced into prominent posterior rib; posterior rib naked 3–5(–10) mm per side; primary lateral veins 3 to 4 pairs, arising at $20^\circ\text{--}50^\circ$, most acutely toward apex, moderately arcuate; secondary veins weakly quilted-sunken on upper surface, in part raised and otherwise prominulous on lower surface, concolorous, drying weakly raised, usually darker than surface; tertiary veins mostly weakly raised, otherwise prominulous on lower surface, drying entirely or in part raised or prominulous, usually darker than surface; reticulate veins prominulous on lower surface, concolorous, drying in part prominulous, otherwise flat, visible, distinct, concolorous to weakly darker than surface; collective veins 3, the innermost arising from apex of posterior rib or occasionally from one of the lateral veins on the inner side of the posterior lobe, moderately scalloped, 4–7 mm from margin. INFLORESCENCES erect, 3 to 5 per axil, odorless; sympodium held within sympodial cataphyll; sympodial cataphyll $5\text{--}8 \times 1\text{--}1.5$ cm, acuminate at apex, obtusely or acutely 1- to 2-ribbed abaxially, pale to medium green; peduncle $3\text{--}6.5$ cm \times ca. $1\text{--}2.5$ mm, terete to weakly cylindroid, narrowing toward base, matte, pale to pale-medium green, drying ca. 1 mm diam., matte, dark brown; **spathe** erect, 4–9.3 cm long (1–4 cm longer than spadix), oblanceolate, acute to weakly acuminate at apex, opening narrowly most of its length at anthesis (to within 1–2 mm of base); spathe tube matte to weakly glossy, medium green, occasionally purplish green on outer surface, weakly glossy to glossy and paler on inner surface, $1.5\text{--}2.4$ cm \times 3–5 mm (to 8 mm diam. at anthesis), drying 2–3 mm diam., matte, dark brown; spathe blade erect to erect-spreading, weakly glossy to semiglossy, pale to medium green or yellow, rarely weakly to prominently purple-tinged on outer surface, weakly glossy to semiglossy and weakly paler on inner surface, $4\text{--}7.3$ cm \times ca. 5 mm, 1.2–1.5 cm wide (flattened), drying matte to weakly glossy, dark brown or reddish brown on outer surface, weakly glossy to semiglossy and weakly paler on inner surface, reflexing after anthesis, frequently forming a coil or spiral with margins out-rolled, marcescent or \pm caducous, quickly deciduous; **spadix** erect, curving forward at anthesis, 4.4–5.7 cm long, sessile, \pm cylindrical, adnate to spathe ca. 6 mm at base, slightly



Figure 41. *Chlorospatha plowmanii* (Madison) Croat & L. P. Hannon. —A. Potted plant, showing the quilted leaf blades and inflorescences seen at center. —B. Stem with petioles visible and a post-anthesal inflorescence that shows the reflexed spathe blade (side view). The reflexed and deciduous spathe blade is only known in this species. —C. Stem with petioles and one inflorescence at anthesis with the spathe blade still erect (frontal view). —D. Axillary cluster of inflorescences, contrasting both pre-anthesal and post-anthesal spathe position with the blades erect and reflexed, respectively. A–C photographed from the cultivar Croat & L. P. Hannon 81475 (MO). D photographed from the SEL live accession of the type collection Plowman *et al.* 3979.

less than 1/2 of the length of pistillate portion; pistillate portion cream, 1–1.5(–2.2) cm \times 2–3 mm, weakly broadest midway; fertile staminate portion cream-colored (rarely yellow), 2–3 cm \times 2–2.5 mm, bluntly to narrowly rounded at apex, weakly tapering; sterile staminate portion white to creamy white (rarely purple-tinged basally), 5–8 \times ca. 2 mm, weakly narrower than pistillate and fertile staminate portions; pistils weakly coherent to \pm laxly arranged, 2 to 3 across the axis (viewed from above), ca. 1 mm long; ovaries cream-colored, 1–1.2 mm diam., \pm cylindrical to obtusely obconical, broadly depressed medially, 2-locular, with pseudoaxile placentation and 6 to 10 ovules per locule, or rarely 1-locular, with basal placentation and 16 to 20 ovules, or with single deeply intrusive parietal placenta; ovules hemianatropous, biseriate, occasionally 3-seriate; funicles shorter than ovule; style Type 1 (Fig. 1), 1–1.2 mm diam., thin, as broad as ovary apex, the margins obscure, not coherent with those of adjacent styles; **stigma** white, ca. 0.2 mm diam., sessile, broadest and truncate at apex; synandria ca. 1 mm long, 1.5–2.5 \times 1–1.5 mm diam. and \pm elongated in direction of axis, coherent, sometimes highly bilaterally symmetrical, sometimes subrounded, prominently and deeply 2- to 3(4)-lobed (occasionally almost to middle), broadly concave medially, with lobes thickened, the margins sinuate-undulate and weakly interlocking with those of adjacent flowers, 2- to 3(4)-androus (mostly 3), the thecae each with a terminal pore; pollen cream-colored, in tetrahedral or linear tetrads, with exine reticulate (Fig. 3G–L); sterile flowers less than 1 mm long, 1.5–2 \times 0.5–1.5 mm diam. and \pm elongated in direction of axis, coherent, truncate, subprismatic to irregularly prismatic, in 3 to 5 whorls. **INFRUCTESCENCE** (Croat *et al.* 88008A) semiglossy, dark purple; berries medium green, purple-spotted at apex and exposed sides; seeds pale green, smooth.

Phenology. *Chlorospatha plowmanii* flowers freely, almost continuously, throughout the year. The species is unique in having a spathe blade that reflexes after anthesis and is then quickly deciduous. Spathe blades that reflex after anthesis have been observed in only two other species, *C. corrugata* and *C. limonensis*. Neither species could be confused with *C. plowmanii*. Inflorescences of *C. plowmanii* are odorless and emerge in quick succession, each reaching anthesis approximately one to three days after anthesis of the preceding inflorescence.

Etymology. *Chlorospatha plowmanii* is named for Timothy C. Plowman (1944–1989), formerly of the Field Museum in Chicago, a renowned Neotropical botanist and collector of many new taxa, including

the type of this species. Plowman was responsible for the successful introduction of countless ornamental plants from a wide variety of families.

Discussion. *Chlorospatha plowmanii* is widespread on the eastern slopes of the Andes in Ecuador, occurring in Morona-Santiago, Napo, Sucumbíos, and Zamora-Chinchipe provinces at 250–1200(–1486) m elevation. Most collections were made in premontane wet forest, but some were made in tropical moist forest, premontane moist forest, or tropical wet forest. The species would be expected to occur northward into Colombia, many collections having been made near that border in the area to the south and north of Lumbaquí, near the type locality. It probably also occurs in Peru, *Jaramillo 14974* having been collected in easternmost Sucumbíos Province, near the Peruvian border.

Chlorospatha plowmanii, a member of *Chlorospatha* sect. *Orientalis*, is found in small colonies and is distinguished by its broadly quilted, subhastate to hastate leaf blades, with the posterior lobes long and narrow, the upper surface velvety, dark green and the lower surface conspicuously reticulate, with all venation glabrous. The petiole is usually sheathed only one fourth of its length. The species is also distinguished by its markedly short peduncle, 3–6.5 cm long and frequently shorter than the spathe. The spathe is usually green, occasionally with the tube purple-tinged, rarely the blade, and the blade yellow. The spadix is less than 6 cm long and usually entirely cream-colored. The morphology of some ovaries is unique in the genus. In several collections, one or two ovaries at the base of the pistillate portion were found to be unilocular with basal placentation, with all other ovaries bilocular with axile or subaxile placentation. The type plant (Plowman *et al.* 3979) is the exception, having most or possibly all ovaries unilocular with basal placentation. All ovaries of this collection were not dissected, but several were examined at different positions along the length of the pistillate portion and found to be unilocular with basal placentation. At present, *C. plowmanii* is the only species in which smooth seeds have been observed, but in only one collection (Croat *et al.* 88008A). This collection is atypical of the species in having more or less sagittate blades and sharply D-shaped petioles that are sulcate throughout and purple-mottled in transverse bands.

Chlorospatha plowmanii would be most easily confused with *C. pubescens*, which is also widespread on the eastern slopes of the Andes in Ecuador, at 400–1400 m elevation. The species appear to be sympatric in all provinces in which both occur. In both species, the leaf blades are broadly quilted,

velvety, dark green on the upper surface, and usually similarly shaped, with the length of the petiole sheath and the size and structure of the inflorescences also similar. The free portion of the petiole of *C. pubescens* is D-shaped, usually sharply so toward the apex, whereas that of *C. plowmanii* is usually terete or subterete. Old petiole bases and cataphylls persist only as short fibers or semi-intact remnants along the stem of *C. plowmanii*, but are more or less intact and cover the stem in *C. pubescens*. *Chlorospatha plowmanii* is entirely glabrous on all its parts, lacking any of the crispy-puberulent to granular-puberulent indumentum that is usually conspicuous in *C. pubescens*. The spathe blade of *C. plowmanii* reflexes after anthesis and is quickly deciduous. In *C. pubescens*, the spathe blade is usually erect after anthesis, only occasionally spreading, and abscises with the fertile staminate portion of the spadix. The synandria of *C. plowmanii* are 2- or 3(4)-androus, thus differing from those of *C. pubescens*, which are (2)3- or 4(5)-androus. The inflorescence of the latter species is sweetly fragrant, whereas that of *C. plowmanii* is odorless.

Madison (1976) published *Caladium plowmanii*, citing *Plowman et al.* 3979 as the type, and in his 1981 treatment of *Chlorospatha*, combined *Caladium plowmanii* Madison and *Caladium longipodum* K. Krause in *Chlorospatha longipoda* (K. Krause) Madison. The type of *Caladium plowmanii* differs from that species in significant ways and is better combined in the new species, *Chlorospatha plowmanii* (see discussion under *C. longipoda*).

Additional specimens examined. ECUADOR. **Morona-Santiago:** Cordillera de Cutucú, Centro Shuar Uusuants/Transkutuku, 600 m, *W. Palacios et al.* 15795 (MO, QCNE). **Napo:** Res. Biol. Jatún Sacha, 8 km from Puerto Misahuallí, rt. side of Río Napo, 450 m, *C. Cerón* 1003 (MO, QAME, QCA, QCNE); 2111 (MO, QCA, QCNE); along Narupa-Coca rd., 4 km E of Narupa (jct. of Baeza-Tena rd.), 1312 m, *Croat et al.* 87833 (AAU, B, BM, BR, CAS, COL, DUKE, F, GH, HUA, INB, JAUM, K, M, MEXU, MO, NY, P, PMA, QCA, QCNE, RSA, S, SEL, TEX, UB, US, VEN); Archidona-San Vicente Para rd., vic. San Pablo, 6.5 km E of Archidona, along Río Ollín, 543 m, *Croat et al.* 88008A (MO, QCNE); Archidona-Baeza rd., 39.9 km N of Archidona, 28.4 km S of Cosanga, 40.8 km S of jct. with Baeza-Papallacta-Lago Agrio rd., 1486 m, *Croat et al.* 88036 (QCNE); along rd. to Mushullacta, 1–5 km S of main Narupa-Coca rd., vic. Parque Nac. Napo-Galeras, 1500 m, *Croat et al.* 96410 (MO). **Sucumbíos:** Zancudo Cocha, vic. of lake, S of & on trail to Río Aguarico, 220 m, *Jaramillo* 14974 (QCA); Cantón Gonzalo Pizarro, Parroquia Gonzalo Pizarro, 8 km S of Recinto Amazonas, 800 m, *Yanez & Shuigra* 846 (QCA). **Zamora-Chinchipe:** vic. El Panguí, hills W of town, 1200 m, *Croat* 87190 (MO, QCNE); Podocarpus Nat. Park, study plot ca. 1 km SW of Bombuscaro Visitors Center, 6 km S of Zamora, 1050 m, *R. Leimbeck et al.* 418 (AAU, QCA).

Cultivated specimens examined. ECUADOR. **Sucumbíos:** along rd. to La Bonita, 6 km N from cut-off at Río Aguarico bridge on Lumbaquí-Lago Agrio rd., 472 m, *Croat & L. P. Hannon* 81496 (MO); 81473 (MO); along rd. to La Bonita, 8 km N of cut-off at Río Aguarico bridge on Lumbaquí-Lago Agrio rd., 487 m, *Croat & L. P. Hannon* 81475 (MO); 31 mi. W of Lago Agrio, *Madison* 3747 (MO, NY, SEL); 4185 (SEL, ex. *Plowman et al.* 3979, GH, MO, P, SEL live acc. #75-0058-001).

56. *Chlorospatha portillae* Croat & L. P. Hannon, sp. nov. TYPE: Ecuador. Zamora-Chinchipe: along El Panguí-Zamora rd., vic. San Roque, 2 km S of San Roque, 10 km S of El Panguí, ca. 900 m, 3°42'11"S, 78°35'59"W, 7 Sep. 2002, *Croat* 87201 (holotype, MO-5771767!; isotypes, AAU!, B!, CAS!, F!, GH!, HUA!, INB!, K!, M!, MEXU!, NY!, QCA!, QCNE!, S!, SEL!, UB!, US!, VEN!). Figure 42A–D.

Herba usque ad 50 cm; internodia 3–8(–10) mm × 1–2.7 cm; cataphylla 14–16.5 cm longa. Petiolus 20.5–42(–53) cm longus, vaginatus per 5–12 cm; lamina foliaris ovata, 20–34.5 × 6–20 cm, nervis primariis lateralibus utroque 5 vel 6. Inflorescentiae 10 in quaque axilla; pedunculus 9–17.5 cm × ca. 1 mm; spatha erecta, 3–5.4 cm longa, tubo 3–4.5 mm diam., lamina complanata 1.6–2.6 cm longa, 2.5–4 mm diam., 7–10 mm lata; spadix 2.3–3.5(–5) cm longus.

Terrestrial herb, to 50 cm tall; stem decumbent, with remnants of old cataphylls persisting ± intact to semi-intact and ± fibrous along its length, occasionally with few bulbils produced; bulbils ovoid, solitary, ca. 9 × 4 mm; sap milky; internodes 3–8(–10) mm × 1–2.7 cm, semiglossy, gray-green, drying matte to weakly glossy, dark brown (all measurements made from dried material); cataphylls 14–16.5 cm long, ± acuminate or obtuse with acumen at apex, 1-ribbed abaxially, pale-medium green, weakly darker maroon-speckled, dark maroon at apex and on abaxial rib, drying weakly glossy to semiglossy, dark reddish brown, weakly fibrous. LEAVES 2 to 4, erect-spreading; **petioles** 20.5–42(–53) cm long, glabrous, semiglossy, dark green, or weakly to prominently maroon-tinged, or entirely dark maroon, drying matte, dark reddish brown, sheathed 5–12 cm, ca. 1/4 of total length; sheath decurrent at apex; free portion 2–5(–9) mm diam. midway, terete or sharply flattened adaxially in apical 3–4 cm, with margins acutely raised and an obtuse medial rib; **blades** narrowly ovate, 20–34.5 × 6–20 cm, (1.3 to) 2.5 to 3.3 times longer than wide, acuminate at apex, broadest at or below middle, acute to rounded at base and frequently weakly inequilateral, occasionally cordulate, decurrent onto petiole, thinly coriaceous, moderately bicolorous, ± symmetrical or weakly to moderately inequilateral, with one side to 2.5 cm wider than opposite side; upper surface quilted,

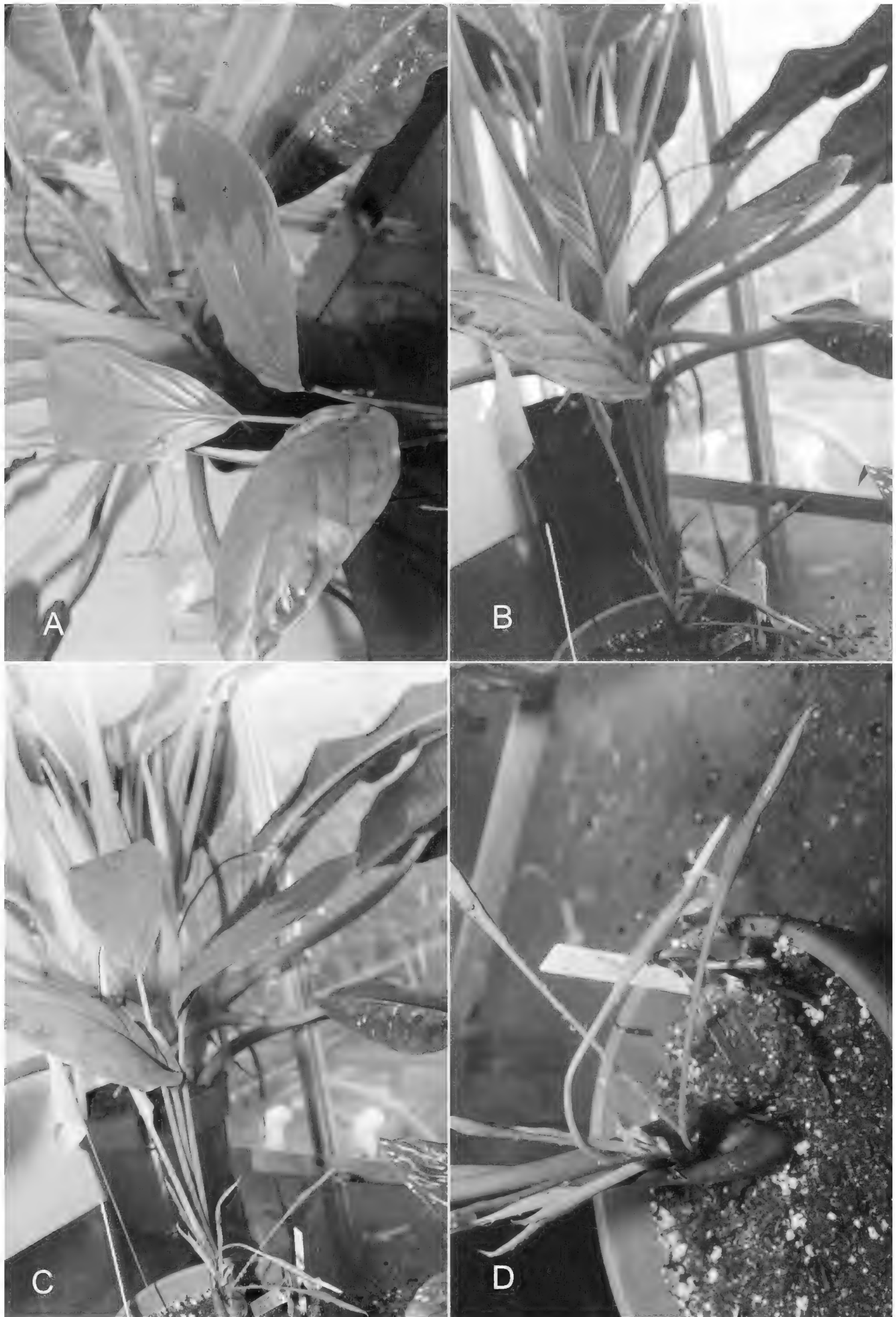


Figure 42. *Chlorospatha portillae* Croat & L. P. Hannon. —A. Close-up of leaf blade adaxial surfaces. —B. Plant habit, potted accession at MO. —C. Sympodia emerging from basal cataphylls, with one post-anthesal inflorescence at right. —D. Stem with nine inflorescences per axil, five immature and stiffly erect, three spreading, one of which is at anthesis. Photographed from the MO cultivar from the paratype Croat 72732.

semiglossy to glossy, dark green, drying weakly glossy, dark brownish green; lower surface glossy, drying semiglossy to glossy, weakly to moderately paler; midrib and major venation deeply sunken and concolorous on upper surface, narrowly raised on lower surface, concolorous or weakly to prominently maroon-tinged, drying \pm flattened, much darker than surface; primary lateral veins 5 to 6 pairs, arising at 25° – 40° , \pm straight to weakly arcuate; minor veins mostly flattened on lower surface, weakly darker than surface, drying concolorous to weakly darker than surface; secondary veins drying weakly prominulous on lower surface; tertiary and reticulate veins flat, visible on lower surface, frequently darker than surface, drying in part visible; collective veins 3 to 4, the innermost arising from base, loop-connected with all preceding lateral veins, moderately scalloped, 5–13 mm from margin. INFLORESCENCES erect, to 10 per axil, the sympodium held within a sympodial cataphyll; sympodial cataphyll 7.4 – $12 \times$ ca. 1.5 cm, acuminate at apex, 1-ribbed abaxially; peduncle 9 – 17.5 cm \times ca. 1 mm, prominently thicker than broad, prominently purple-tinged or weakly to prominently dark purple-mottled, drying matte, blackish brown; **spathe** erect, 3 – 5.4 cm long, acuminate at apex; spathe tube medium green and purple-tinged on outer surface, pale green on inner surface, 1.2 – 2.8 cm \times 3 – 4.5 mm, drying matte, dark brown on outer surface, weakly paler on inner surface; spathe blade medium green and prominently purple-tinged on outer surface, pale green on inner surface, 1.6 – 2.6 cm \times 2.5 – 4 mm, 7 – 10 mm wide (flattened), drying matte, dark brown on outer surface, weakly paler on inner surface, marcescent, erect after anthesis; **spadix** erect, 2.3 – 3.5 (– 5) cm long, sessile, adnate to spathe 0.7 – 1.8 cm at base, $1/2$ to $3/4$ of the length of pistillate portion; pistillate portion white, 1 – 2.4 cm \times 2.2 – 3 mm, broadest near apex, drying dark brown; fertile staminate portion white, 1.1 – 2 cm \times 2 – 3 mm, ellipsoid, narrowly rounded at apex, drying medium yellow-brown; sterile staminate portion white, 3 – $4 \times$ 1 – 1.5 mm, cylindrical, drying pale-medium yellow-brown; pistils densely arranged, ca. 3 to 4 across the axis (viewed from above), 1.5 – 2 mm long; ovaries ovoid to \pm cylindrical, ca. 1.5×1 mm, 2-locular, with axile placentation; ovules 8 to 10 per locule, hemianatropous, biseriate; funicles shorter than ovules; style Type 2 (Fig. 1), 0.3 – $0.5 \times$ ca. 0.8 mm, comprising ca. $1/4$ of the length of pistil, as broad as ovary apex, the margins obscure and weakly or not at all coherent with those of adjacent styles; **stigma** ca. 0.2 mm diam., capitate, weakly elevated on narrowed portion of style, drying dark brown; synandria ca. $1 \times$ ca. 1 mm, coherent, truncate, 2- to

3-lobed, 2- to 3-androus; sterile flowers ca. $0.5 \times$ ca. 0.8 mm, coherent, truncate, subprismatic to prismatic, in 3 whorls. Berries not known.

Phenology. Flowering is only known to occur in *Chlorospatha portillae* during the months of July and September.

Etymology. *Chlorospatha portillae* is named for José (Pepe) Portilla Andrade, owner of Ecuagenera in Gualaceo, Ecuador, benefactor of our work with Araceae in Ecuador, and noted expert on Ecuadorian Orchidaceae. The species was collected near Portilla's hometown of El Panguí, Ecuador, and it is named in his honor for his support of our work with Ecuadorian Araceae.

Discussion. *Chlorospatha portillae* is known from five collections made in premontane wet forest on the eastern slopes of the Andes in Zamora-Chinchipe Province, Ecuador, at 875 – 1465 m elevation, with most made in the vicinity of El Panguí. The type was collected 10 km south of El Panguí, the other collections to the west and south of the type locality. The localities lie near the borders with Morona-Santiago Province and Peru, and the species would be expected to occur to the north in that adjoining province and possibly eastward into Peru. However, these sites are on the western side of the Cordillera del Cóndor, the summit of which follows the border between the two countries and possibly serves as a barrier to eastward distribution.

Chlorospatha portillae is a member of *Chlorospatha* sect. *Orientales* and is distinguished by its glossy, dark green, narrowly ovate leaf blades that are acute, rounded, or cordulate at the base, a shape not known in any other species from the eastern slopes of the Andes. The species is also distinguished by having 10 inflorescences per sympodium, the maximum number observed in the genus, with the sympodium held within a sympodial cataphyll, and by its small, purplish spathes (3 – 5.4 cm long). The synandria are truncate at the apex, an unusual condition in species from the eastern slopes in Ecuador. The pistils of this species are similar to those of only two species, *C. cutucuensis* and *C. sizemoreae*, also from the eastern slopes of the Andes in Ecuador, with the ovaries elongated and somewhat cylindrical or ovoid and the styles briefly attenuated and lacking a mantle. In *C. cutucuensis* and *C. sizemoreae*, the inflorescences are held within the petiole sheath, whereas in *C. portillae*, the inflorescences are held within a sympodial cataphyll toward the base of the petiole. Vegetatively, the two species are quite different from

C. portillae, both having more or less prominent posterior lobes.

Chlorospatha portillae could not be confused with any known species of *Chlorospatha*. Vegetatively, it most closely resembles *C. oblongifolia* from the western slopes of the Andes in Chocó Department in northern Colombia (see discussion under *C. oblongifolia*).

Paratypes. ECUADOR. **Zamora-Chinchipe:** along Zamora–Gualaquiza rd., 70.9 km N of bridge over Río Zamora in Zamora, betw. Los Encuentros & El Panguí, 935 m, 3°42'S, 78°25'W, 4 Mar. 1992, *Croat* 72732 (MO [cult. at MO, cf. Fig. 42]); Los Encuentros–El Sarsa rd., Km. 14.7, 1455 m, 3°48'40"S, 78°36'28"W, 15 July 2004, *Croat, L. P. Hannon, G. Wahlert & T. Katan* 91089 (MO, QCNE); along rd. from near Paquisha, S to Las Orquídeas, & end of rd. at Río Nangaritzza, via Guayzimi, beginning at 15.9 km E of Zumbi & Río Zamora, then 47 km S of intersection near Paquisha, 2.6 km N of Las Orquídeas, 875 m, 4°12'48"S, 78°38'41"W, 17 July 2004, *Croat, L. P. Hannon, G. Wahlert & T. Katan* 91343 (MO, QCNE); betw. San Carlos & Nambija, on mining rd. E off of main San Carlos–Nambija rd. beginning 6 km S of San Carlos, 0.9 km up rd. toward mining operation at end of rd., 2.4 km from rd., 1465 m, 4°02'18"S, 78°47'52"W, 23 July 2004, *Croat, L. P. Hannon, G. Wahlert & T. Katan* 91999 (MO, QCNE).

57. *Chlorospatha pubescens* Croat & L. P. Hannon, sp. nov. TYPE: Ecuador. Napo: along Archidona–San Vicente Para rd., 15.8 km E of Archidona, 5.7 km E of Santo Domingo, 10 km E of San Pablo, 797 m, 0°57'24"S, 77°43'49"W, 23 Apr. 2003, *Croat, L. P. Hannon & N. Altamirano* 88000 (holotype, MO-5692342!; isotypes, B!, COL!, K!, NY!, QCNE!, S!, US!). Figure 43A, B.

Herba minus quam 50 cm; internodia 0.8–2 × 1–1.5 cm; cataphylla 7–13 cm longa. Petiolus (13–)16–29(–32) cm longus, vaginatus per 5–10(–14) cm; lamina foliaris hastata vel subhastata, interdum sagittata, (12.5–)15–21.5(–27) × (10–)12.5–19.5 cm, lobis posterioribus 5–10(–11.5) × (3–)3.5–6.5 cm, nervis basalibus utroque 1 vel 2(3), nervis primariis lateralibus utroque 3 vel 4. Inflorescentiae (1 ad)3 ad 6 in quaque axilla cataphyllo sympodiali 5–8 cm longo cinctae; pedunculus (3.5–)4.5–7(–8.5) cm × 1–1.5 mm; spathe 4.3–7(7.1) cm longa, tubo 3–6 mm diam., lamina complanata (2.5–)3.2–5.2(–5.5) × 1.2–1.8 cm; spadix 3.3–4.3(–4.6) cm longus.

Terrestrial herb, less than 50 cm tall, in small colonies; stem decumbent, erect 10–15 cm at apex, with remnants of old cataphylls persisting ± intact along its length, occasionally producing bulbils along its length; bulbils solitary, green, 2–3 × 2–3 mm; internodes 0.8–2 × 1–1.5 cm, weakly glossy to semiglossy, dark green or yellow-green, drying 7–10 mm diam., matte to weakly glossy, medium to dark brown or green; cataphylls 7–13 cm long, cuspidate

at apex, rarely obtuse with apiculum (apiculum 3–15 mm long), entirely acutely or bluntly 1- to 2-ribbed or in part only toward apex, usually entirely densely crispy-puberulent in minutely spaced longitudinal rows, or sparsely, crispy-puberulent along rib(s) and some veins, matte to weakly glossy, medium green, drying matte to weakly glossy, medium to dark brown. LEAVES (2 to)6 to 8, erect, erect-spreading, spreading to reflexed-spreading; **petioles** (13–)16–29(–32) cm long, minutely obtusely many-ribbed abaxially, usually crispy-puberulent along ribs, frequently more densely so or scurfy-pubescent in apical 3–4 cm, rarely only near apex, occasionally entirely granular-puberulent, matte, medium to dark green, drying matte, (medium) dark brown or greenish, sheathed 5–10(–14) cm, 1/10 to 1/4(1/3 to 1/2) of its length; sheath with sides ± erect, decurrent at apex, or with one side wider and prominently free-ending (free-ending portion 5 mm long, acute at apex), glossy and paler on inner surface; free portion 5–7 mm diam. midway (drying 2–5 mm diam.), obtusely D-shaped, the margins acute toward apex, rarely entirely sharply D- or U-shaped, obtusely or narrowly and shallowly sulcate, rarely narrowly triangular sulcate with flared margins concave in apical 4 cm; **blades** hastate or subhastate, occasionally sagittate, (12.5–)15–21.5(–27) × (10–)12.5–19.5 cm, 1.1 to 1.4 times longer than wide, weakly acuminate to apiculate at apex, rarely bluntly acute, broadest at base (rarely broadest across anterior lobe), 1.5 to 1.9(to 2.3) times broader at base than across anterior lobe (measured tip to tip across posterior lobes), thin to thinly coriaceous, conspicuously bicolorous (rarely moderately bicolorous), the margins broadly undulate, rarely crispate-undulate; upper surface broadly quilted, rarely flat, velvety, dark green, drying matte or velvety-matte, dark green (rarely dark yellow-brown); lower surface reticulate, matte, narrowly colliculate along all venation, drying weakly glossy to semiglossy, moderately to prominently paler (rarely weakly paler); anterior lobe (8.5–)10.5–18(–19.5) × (5.5–)7.5–12.5(–15.5) cm, (1.3)1.4 to 1.6(to 1.9) times longer than wide, (1.5 to)1.7 to 2.2(to 2.5 to 2.7) times longer than posterior lobes, broadest near base, weakly or not at all constricted at base, rarely moderately to prominently constricted, ± symmetrical; posterior lobes directed outward, 5–10(–11.5) × (3–)3.5–6.5 cm, (1.2 to)1.4 to 2.3(to 2.5) times longer than wide, bluntly acute to narrowly rounded at apex, broadest midway or near base, rarely weakly constricted at base, ± symmetrical, rarely weakly or moderately inequilateral, the inner side narrower, weakly to broadly rounded toward base and briefly attenuate



Figure 43. A, B. *Chlorospatha pubescens* Croat & L. P. Hannon. —A. Live plant from the paratype collection L. P. Hannon 02-071 (ABG-911415). —B. Herbarium specimen, Palacios 4795 (MO-4373109, sheet 1 of 2). C, D. *Chlorospatha ricaurtensis* Croat & L. P. Hannon, photographed from the type collection Croat 71405 (MO-3789359). —C. Fertile habit. —D. Close-up, showing erect inflorescence.

onto posterior rib, rarely decurrent onto petiole; outer side straight to weakly concave toward base, rarely 1.2 to 2.3 times wider than inner side midway; all orders of venation usually \pm crispy-puberulent to prominently granular-puberulent on lower surface, most densely so toward base of midrib, major veins and entire length of posterior rib; midrib deeply sunken on upper surface, occasionally entirely sparsely crispy-puberulent or in part only in basal 1/2, concolorous or weakly paler than surface and yellow-green, drying concolorous or weakly to moderately paler, round-raised or occasionally obtusely angular on lower surface, minutely many-ribbed, weakly paler to weakly darker than surface, drying weakly raised to \pm flattened, concolorous or weakly darker than surface; **basal veins** 1 to 2(3) pairs, coalesced into prominent posterior rib, the first free to the base, or with 3 to 6 branching off, the first free to the base, 1 to 2 acroscopic, 2 to 3 basiscopic, coalesced into weak posterior rib 3–4 cm long; posterior rib naked 3–8 mm per side (rarely not naked), round-raised with an acute medial rib on lower surface, finely many-ribbed, frequently \pm scurfy-pubescent, drying raised, darker than surface; primary lateral veins 3 to 4 pairs, arising at 15°–45°(–70°), most acutely toward apex, straight or moderately arcuate, deeply quilted-sunken (rarely etched-sunken) on upper surface, occasionally entirely sparsely crispy-puberulent or in part in basal 1/4 to 1/2, drying concolorous, or in part concolorous and otherwise weakly to moderately paler in basal 1/2, round-raised on lower surface, occasionally acutely or obtusely angular, minutely many-ribbed, weakly paler to weakly darker than surface, drying weakly raised and weakly flattened, concolorous or weakly darker than surface; secondary veins in part weakly sunken or obtusely sunken on upper surface, convex to narrowly raised on lower surface, concolorous to weakly darker than surface, drying raised or narrowly raised, concolorous to weakly darker than surface; tertiary veins usually obscure on upper surface, rarely obtusely sunken, entirely raised on lower surface, or in part raised and otherwise prominulous, concolorous to weakly darker than surface, drying entirely raised or in part raised and otherwise prominulous, weakly darker than surface; reticulate veins usually obscure on upper surface, rarely obtusely sunken, entirely prominulous on lower surface, or mostly prominulous and otherwise visibly distinct and flat, weakly darker than surface, drying entirely or in part prominulous and otherwise flat, weakly darker than surface; collective veins 2 to 4, the innermost arising from one of the lowermost lateral veins on inner side of posterior lobe, occasionally from apex of posterior rib,

loop-connected with all preceding lateral veins, weakly to moderately scalloped, 4–10(–16) mm from margin. INFLORESCENCES erect, (1 to)3 to 6 per axil, emitting a weak, sweet fragrance at anthesis; sympodium held within a sympodial cataphyll; sympodial cataphyll 5–8 cm long, pale-medium green, usually weakly crispy-puberulent or granular-puberulent along longitudinal veins (rarely glabrous), drying matte to weakly glossy, medium brown; peduncle (3.5–)4.5–7(–8.5) cm \times 1–1.5 mm, terete, or cylindroid and wider than thick, to 2.5 mm wide and 1.5 mm thick, rarely obtusely triangular and flattened adaxially, narrowest at base, matte, pale to medium-dark green (rarely creamy white or entirely or in part deeply purple-tinged), sparsely crispy-puberulent or granular-puberulent in longitudinal rows (rarely glabrous), drying matte to weakly glossy, medium to dark brown or greenish brown; **spathe** erect, frequently weakly cucullate, 4.3–7(7.1) cm long, usually entirely greenish cream, pale green or medium-pale green on both surfaces, rarely \pm deeply purple-tinged on outer surface, most prominently so on tube, oblanceolate, cuspidate at apex, opening narrowly or broadly most of its length at anthesis, the margins directed forward or weakly outward; spathe tube weakly glossy (semiglossy) on outer surface, \pm narrowly, sparsely crispy-puberulent or granular-puberulent at base (rarely entirely glabrous), weakly glossy (glossy) on inner surface, (1–)1.5–1.9 cm \times 3–6 mm, weakly thicker than broad, drying 2–4 mm diam., matte to weakly glossy, medium to dark brown or greenish on outer surface, paler on inner surface; spathe blade erect to erect-spreading, matte (semiglossy) on outer surface, matte (glossy) on inner surface, (2.5–)3.2–5.2(–5.5) cm long, 1.2–1.8 cm wide (flattened), obtusely 1-ribbed with most venation prominulous on outer surface, drying matte (rarely weakly glossy), medium to dark brown on both surfaces, usually weakly to moderately paler than tube, marcescent, usually erect after anthesis, rarely spreading; **spadix** erect, curving forward at anthesis, 3.3–4.3(–4.6) cm long, usually weakly stipitate ca. 1 mm at base (stipe and axis pale green), occasionally sessile, \pm cylindrical, adnate to spathe 2–3(–5) mm at base, along stipe and narrowly onto pistillate portion 2–3 mm, 1/4 or less of the length of pistillate portion, rarely to 1/2 of the length (*L. P. Hannon et al.* 97-365); pistillate portion cream or pale yellow-green, 0.8–1.7 cm \times 1.5–3 mm, broadest midway; fertile staminate portion white, cream, or creamy yellow, 1.2–2.3(–2.5) cm \times 2–3 mm, bluntly acute to narrowly rounded at apex, broadest at base, \pm cylindrical to weakly tapering; sterile staminate portion cream or rarely white and weakly purple-

tinged or minutely purple-speckled, $3-8(-10) \times 2-2.5$ mm, \pm cylindrical or weakly broadest at apex or base, occasionally naked at base to 1 mm; pistils weakly coherent to \pm laxly arranged (most conspicuously so toward base), 2 to 4 across the axis (viewed from above), 1–1.3 mm long; ovaries cream, 1–1.5 mm diam., \pm cylindrical to obtusely obconical, frequently broadly depressed medially, 2-locular, with axile or subaxile placentation, 5 to 8(to 10) ovules per locule, or rarely 1-locular with subaxile placentation and ca. 12 ovules; ovules hemianatropous, biseriate; funicles shorter than ovule; style Type 1 (Fig. 1), (0.8–) 1–1.2 mm diam., weakly narrower than to as broad as ovary apex, with red chromoplasts, the margins distinct, not coherent with those of adjacent styles; **stigma** white, 0.2–0.3 mm diam., sessile, \pm capitate or cylindrical, rarely broadest and truncate at apex; synandria ca. 1 mm long, $(1.3-1.8-2) \times (0.8-1.3-1.5)$ mm diam. and \pm elongated in direction of axis, occasionally highly bilaterally symmetrical, sometimes subrounded, prominently and deeply (2)3- to 4(5)-lobed, occasionally almost to middle (rarely [2]3-lobed, on one inflorescence), broadly concave medially, with lobes prominently thickened, the margins sinuate-undulate and interlocking with those of adjacent flowers, coherent, (2)3- to 4(5)-androus, the thecae each with a terminal pore; pollen cream-colored, in tetrahedral tetrads, with exine reticulate; sterile flowers, 0.7–1 mm long, $1.5-2 \times (0.5-1.2)$ mm diam. and \pm elongated in direction of axis, less so in basal whorl, coherent, truncate, subprismatic to irregularly subprismatic, in 3 to 5(6) whorls. Berries not known.

Phenology. Flowering is known to occur in *Chlorospatha pubescens* during all months except February and June, and probably occurs throughout the year. The sympodial leaf is a cataphyll rather than a fully expanded foliage leaf, an unusual character state in *Chlorospatha*. Inflorescences are fragrant and emerge in quick succession, each reaching anthesis approximately one to three days after anthesis of the preceding inflorescence.

Etymology. The epithet is taken from the Latin “pubescens,” meaning “hairy,” referring to the conspicuous puberulent indumentum usually encountered on the cataphyll, petiole, peduncle, spathe tube, and veins on the lower surface of the leaf blade of *Chlorospatha pubescens*.

Discussion. *Chlorospatha pubescens* is widespread on the eastern slopes of the Andes in Ecuador, occurring in Morona-Santiago, Napo, Pastaza, Sucumbíos, and Zamora-Chinchipe provinces at

400–1551 m elevation, with most collections from Napo and Pastaza. The various collection sites are widely separated, and the species would be expected to occur in intervening areas. The species would also be expected to occur in Peru, possibly northward into Putumayo Department, Colombia. *Chlorospatha pubescens* has been collected in tropical wet forest, premontane wet forest, premontane rainforest, and rarely in premontane moist forest.

Chlorospatha pubescens is a member of *Chlorospatha* sect. *Orientales*. Although blade shape is somewhat variable in this section, the species is distinguished by its usually prominently hastate leaf blades that are velvety, dark green, and usually broadly quilted on the upper surface and much paler and conspicuously reticulate on the lower surface, with all venation more or less raised and crispy-puberulent to granular-puberulent. This indumentum usually extends the full length of the petiole, occasionally becoming scurfy-pubescent near the apex and on the posterior rib, and is usually found also on the peduncle and the base of the spathe tube. The petiole sheath is short in most collections, comprising one tenth to one fourth of the total length, occasionally one third to one half of the length. The entire length or basal half of the midrib and major venation are occasionally sparsely crispy-puberulent on the upper surface, a condition observed in no other species. The peduncle is short (4.5–7 cm long) and the inflorescence is small (4.3–7 cm long) and usually pale green, with the spathe blade marcescent and erect after anthesis (rarely spreading). The spadix is usually weakly stipitate. The synandria are unusual for a species from the eastern slopes of the Andes in occasionally being 5-androus, although most are 3- to 4-androus.

Chlorospatha pubescens would be most easily confused with *C. plowmanii*, which is also widespread on the eastern slopes of the Andes in Ecuador, at 220–1050(–1200) m elevation. The species appear to be sympatric in all provinces in which both occur (see discussion under *C. plowmanii*).

Chlorospatha pubescens could possibly be confused with *C. engleri*, known only from the type collection made along the Macas–Riobamba road in the Parque Nacional Sangay in Morona-Santiago Province, Ecuador, on the eastern slopes of the Andes, at 1659 m elevation (see discussion under *C. engleri*).

Paratypes. ECUADOR. **Morona-Santiago:** along Gualaquiza–Limón rd., vic. Indanza, ca. 1200 m, $3^{\circ}02'10''\text{S}$, $78^{\circ}28'28''\text{W}$, 8 Sep. 2002, Croat 87329 (MO, QCNE); Méndez–Paute rd., 43.7 km W of Méndez, 1551 m, $2^{\circ}36'36''\text{S}$, $78^{\circ}28'12''\text{W}$, 12 July 2004, Croat, L. P. Hannon, G. Walther & T. Katan 90932 (MO, QCNE). **Napo:** Tena–Puyo rd., Río Napo, Añangu, 550 m, 18–19 July

1982, *L. Besse*, *H. Kennedy* & *R. Baker* 1638 (SEL); Tena-Puyo rd., 61.5 km N of Puyo, 500 m, 22 Dec. 1979, *Croat* 49647 (MO); Archidona-Baeza rd., 5 km S of turn-off to Loreto, 1033 m, 0°45.924'S, 77°47.545'W, Apr. 2003, *Croat*, *L. P. Hannon* & *N. Altamirano* 87803 (MO, QCNE); Cantón Tena, Est. Biol. Jatún Sacha, Río Napo, 8 km E of Misahuallí, 400 m, 1°04'S, 77°36'W, 8 Jan. 1990, *W. Palacios* 4795 (MO-4373109 [sheet 1], MO-4373110 [sheet 2], QCNE). **Pastaza:** Hac. San Antonio von Humboldt, 2 km NE of Mera, 1300 m, 1°27'S, 78°06'W, *R. Baker et al.* 5795 (MO, NY, QAME, QCNE); along rd. to Río Anzu, trail W into mtns., 1238–1400 m, 1°23'27"S, 78°03'19"W, 6 May 2003, *Croat*, *L. P. Hannon* & *M. Menke* 88730 (B, CAS, MEXU, MO, NY, QCNE); along Mera-Río Anzu rd., 7.7 km N of Río Alpayacu, 1267 m, 1°25'51"S, 78°04'34"W, 8 May 2003, *Croat*, *L. P. Hannon* & *M. Menke* 88813 (K, MO, QCNE, US). **Sucumbíos:** along rd. to La Bonita, 8 km N of cut-off at Río Aguarico bridge, N of Lumbaquí on Baeza-Lago Agrio rd., 487 m, 0°04'18"N, 77°21'42"W, Mar. 1997, *L. P. Hannon* 97-365 (CUVC, GB, GH, HUA, INB, MO). **Zamora-Chinchipe:** vic. El Panguí, Quime crossing Río Zamora, 861 m, 3°32'28"S, 78°26'40"W, Mar. 1996, *Croat* & *L. P. Hannon* 81351 (MO); along rd. from Quime Ferry crossing into Cordillera de Cóndor, 22 km SW of Río Zamora, & Quime crossing, 1489 m, 3°37'46"S, 78°26'17"W, 14 July 2004, *Croat*, *L. P. Hannon*, *G. Walther* & *T. Katan* 91068 (MO, QCNE); along rd. betw. Zumbi on Río Zamora & summit of Cordillera del Cóndor, 27.3 km E of Zumbi, 8.6 km E of Río Nangaritza bridge, 1259 m, 3°56'17"S, 78°37'45"W, 16 July 2004, *Croat*, *L. P. Hannon*, *G. Walther* & *T. Katan* 91229 (MO, QCNE).

Cultivated specimens examined. ECUADOR. **Napo:** Tena-Puyo rd., *T. Plowman* 14063 (F, K, ex. *L. Besse et al.* 1638, SEL live acc. 82-517). **Pastaza:** Vic. Puyo, *L. P. Hannon* 02-071 (MO, ex. *M. McGovern s.n.*, ABG live acc. 911415).

58. *Chlorospatha queremalensis* Croat & L. P. Hannon, sp. nov. TYPE: Colombia. Valle: along Old Calí-Buenaventura rd., betw. Queremal & Anchicayá, departing rd. on trail at Km. 55, 6.5 km W of Queremal via Río San Juan, 1250 m, 3°32'23"N, 76°45'26"W, 26 July 1997, *Croat* & *J. Gaskin* 80373 (holotype, MO-04937477!; isotype, CUVC not seen). Figure 44A.

Herba minus quam 1 m; cataphylla ca. 20 cm longa. Petiolus ca. 59 cm longus; lamina foliaris anguste ovata, cordato-sagittata, ca. 38 × 21.5 cm, lobis posterioribus 10.4–10.5 × 9–10 cm, nervis basalibus utroque 7 ad 9, nervis primariis lateralibus utroque 8 vel 9. Inflorescentia ignota.

Terrestrial herb, less than 1 m tall; stem to 39 cm long, with remnants of old cataphylls persisting ± intact to semi-intact and ± fibrous at upper nodes, otherwise as short, pale fibers; internodes (1.7–)2–4 cm × to 2.7 mm, dark green, becoming brown with age, drying matte to weakly glossy, dark reddish brown (all measurements made from dried material); cataphylls ca. 20 cm long, apex not known, drying

semiglossy to glossy, dark reddish brown. LEAVES 1; **petiole** ca. 59 cm long, ± spongy, glabrous, weakly glossy, dark green, drying semiglossy, dark blackish brown; sheath not determined; free portion ca. 5 mm diam. midway, terete; **blade** narrowly ovate, cordate-sagittate at base, 38 × 21.5 cm (12.5 cm wide at base), 1.8 times longer than wide, weakly acuminate at apex, broadest across anterior lobe, 1.7 times wider across anterior lobe than at base (measured tip to tip across posterior lobes), subcoriaceous, moderately bicolorous; upper surface weakly glossy, dark green, drying semiglossy, blackened gray-green; lower surface weakly glossy, drying weakly glossy to semiglossy, weakly paler; anterior lobe 27.8 × 21.5 cm, 1.3 times longer than wide, 2 times longer than posterior lobes, broadest below middle; posterior lobes directed toward base, 10.4–10.5 × 9–10 cm, weakly longer than wide, narrowly rounded at apex, broadest at base, markedly inequilateral, the inner side narrower, weakly rounded toward base and briefly attenuate onto posterior rib; outer side 3.2 to 4.6 times wider than inner side midway, convex or weakly concave toward base; sinus ± oblong; midrib and major venation sunken on upper surface, glabrous on lower surface, darker than surface, drying ± flattened, moderately darker than surface; midrib round-raised on lower surface; **basal veins** 7 to 9 branching off, 5 to 6 acroscopic, 3 to 4 basiscopic, the first free to the base, fourth and fifth coalesced 3–6 cm into a moderately prominent posterior rib 9 cm long; posterior rib naked ca. 1 cm per side; primary lateral veins 8 to 9 pairs, arising at 40°–70°, most acutely toward apex, moderately arcuate, convex on lower surface; secondary veins raised on lower surface, drying raised, weakly to moderately darker than surface; tertiary veins visible and distinct on lower surface, drying distinct, in part weakly prominulous to weakly raised, otherwise flat, concolorous to weakly darker than surface; reticulate veins drying obscure; collective veins 3, the innermost arising from one of the lowermost lateral veins on inner side of posterior lobe, loop-connected with all preceding lateral veins, parallel to and 2–4 mm from margin. INFLORESCENCE not known. Berries not known.

Phenology. Flowering is not known in *Chlorospatha queremalensis*.

Etymology. *Chlorospatha queremalensis* is named for Queremal in Valle Department of Colombia where the type specimen was collected.

Discussion. *Chlorospatha queremalensis* is known only from the sterile type collection made in Valle Department, Colombia, along a trail departing the old

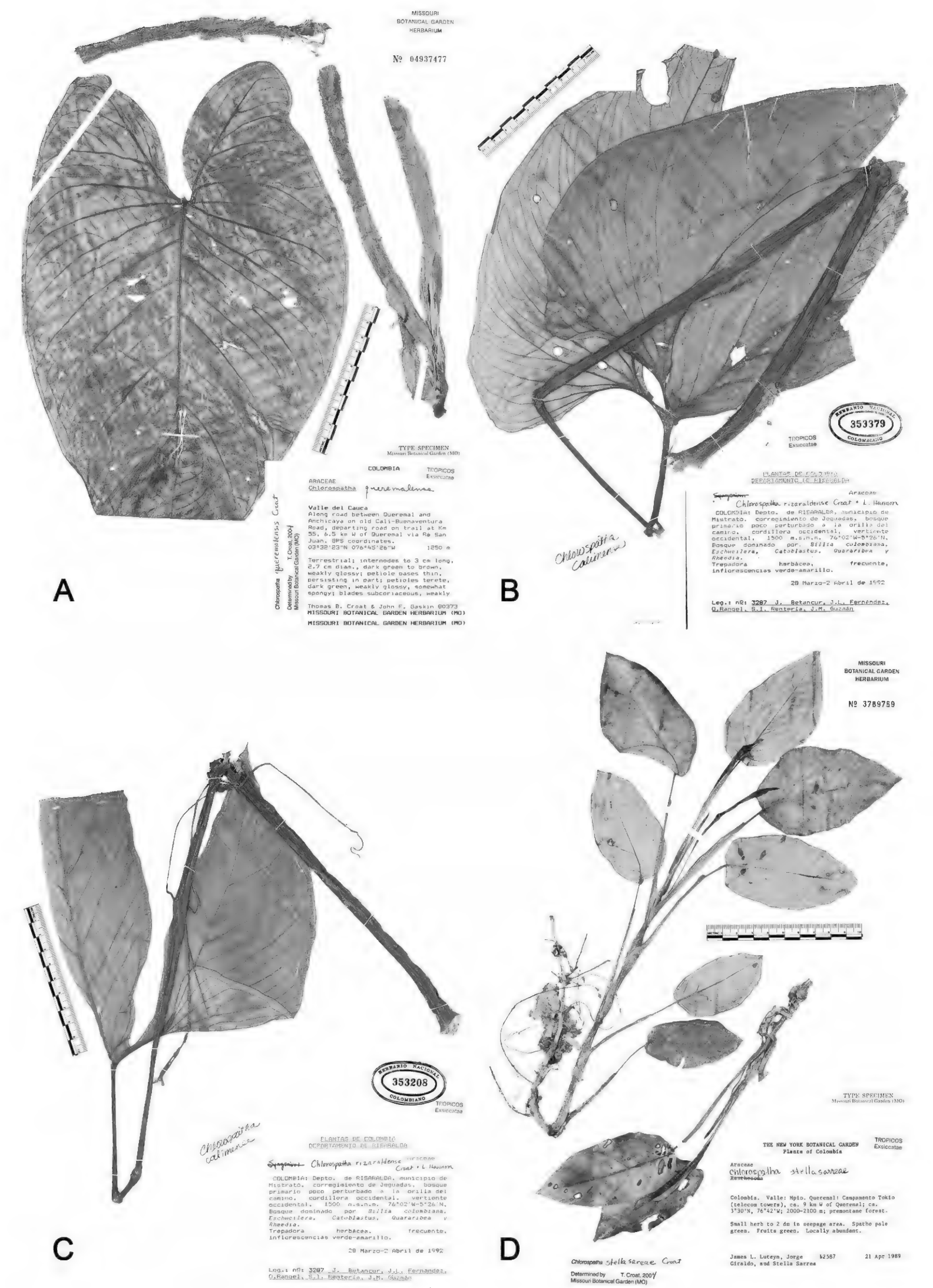


Figure 44. —A. *Chlorospatha queremalensis* Croat & L. P. Hannon, holotype Croat & Gaskin 80373 (MO-4937477). B, C. *Chlorospatha risaraldensis* Croat & L. P. Hannon, holotype Betancur et al. 3287 (MO). —B. Isotype of *C. risaraldensis* (COL-353379). —C. Holotype of *C. risaraldensis* (COL-353379). —D. *Chlorospatha stellasareae* Croat & L. P. Hannon, holotype Luteyn et al. 12587 (MO-3789759).

road from Calí to Buenaventura at Km. 55, 6.5 km west of Queremal, between Queremal and Anchicayá, at 1250 m elevation, in tropical wet forest on the western slopes of the Cordillera Occidental. The species would be expected to occur elsewhere within the department.

Chlorospatha queremalensis is a member of *Chlorospatha* sect. *Occidentales* and is distinguished by its long internodes (2–4 cm long) and subcoriaceous, dark green, narrowly ovate leaf blades that are cordate-sagittate at the base and dry blackened, gray-green, with short, broad posterior lobes that are narrowly rounded at the apex. The species is also characterized by its numerous primary lateral veins (eight to nine pairs), a feature that distinguishes it from the relatively few species with similarly shaped blades, from the western slopes in Colombia and Ecuador: *C. besseae*, *C. bogneri*, *C. macphersonii*, and species indet. 1. *Chlorospatha besseae*, *C. bogneri*, and species indet. 1 occur only in the frontier region along the border between Colombia and Ecuador, the last two species in Nariño Department, Colombia, and the first in northern Ecuador. *Chlorospatha macphersonii* occurs only in Antioquia Department, Colombia, to the north, on the eastern slopes of the Cordillera Occidental. These four species have between three and five pairs of primary lateral veins, rarely six pairs. The blades of *C. queremalensis* are significantly larger than those of the aforementioned species, with the upper surface smooth and weakly glossy. The blades of *C. besseae* and species indet. 1 are velvety, those of *C. bogneri* rugose, and those of *C. macphersonii* bullate.

59. *Chlorospatha ricaurtensis* Croat & L. P. Hannon, *Aroideana* 33: 84–86. 2010. TYPE: Colombia. Nariño: Res. Nat. La Planada, 7 km above Chucunés, on Túquerres–Ricaurte rd., along La Rosa–Potrero de Hermogenes trail, 1800–1850 m, 1°06'N, 77°53'W, 13 Mar. 1990, Croat 71405 (holotype, MO-3789359!; isotype, PSO not seen). Figure 43C, D.

Terrestrial herb, ca. 50 cm tall; stem with remnants of old leaf bases and cataphylls persisting \pm intact along its length; internodes 1–1.5 \times 1.5–2.3 cm, semiglossy, medium green, drying matte to weakly glossy, dark greenish brown (all measurements made from dried material); cataphylls 20–24 cm long, cuspidate at apex, drying weakly glossy to semiglossy, medium-dark to dark reddish brown. LEAVES 2 to 5, erect-spreading; **petioles** 36–49 cm long, glabrous, medium green, purple-tinged, most prominently so toward base, drying matte, dark reddish brown to occasionally almost black, sheathed

21–31 cm, ca. 2/3 of total length; sheath free-ending at apex; free portion ca. 3 mm diam. midway, obtusely angular; **blades** sagittate, weakly subhastate on drying, 24–25 \times 13 cm, 1.8 to 1.9 times longer than wide, abruptly acuminate at apex, broadest at base, 1.3 to 1.7 times wider at base than across anterior lobe (measured tip to tip across posterior lobes), thinly coriaceous, moderately bicolorous; upper surface semiglossy, dark green, drying semiglossy, dark brownish green; lower surface semiglossy, drying weakly glossy, in part semiglossy, moderately paler; anterior lobe 14–14.2 \times 7.5–10 cm, 1.4 to 1.9 times longer than wide, 1.1 to 1.4 times longer than posterior lobes, broadest at or below middle, moderately inequilateral, with one side 1 cm wider than opposite side; posterior lobes directed toward the base, 10–12.5 \times 4–4.5 cm, 2.2 to 3 times longer than wide, narrowly rounded at apex, broadest at or below middle, \pm symmetrical, the inner side broadly rounded toward base, briefly to moderately attenuate onto posterior rib; outer side \pm straight toward base; midrib and major veins paler than upper surface, round-raised on lower surface, paler than surface, drying prominently darker than surface; midrib sunken on upper surface, drying raised on lower surface; **basal veins** 4 to 6 pairs, coalesced into a prominent posterior rib; posterior rib naked 1–1.2 cm per side; primary lateral veins 3 pairs, arising irregularly at 35°–50°, strongly arcuate, occasionally in part irregularly ascending, narrowly sunken on upper surface, drying weakly raised and \pm flattened on lower surface; secondary veins in part obtusely sunken on upper surface, raised on lower surface, drying weakly raised, weakly to moderately darker than surface; tertiary veins visible, distinct on lower surface, darker than surface, drying distinct, in part weakly prominulous, otherwise flat, weakly darker than surface; reticulate veins drying obscure; collective veins 3, the innermost arising from one of the lowermost lateral veins on inner side of posterior lobe, \pm parallel to and 3–7 mm from margin. INFLORESCENCES erect, to 3 per axil; peduncle held within the sheath, 23–31 cm \times 3–4 mm, drying weakly glossy, dark blackish brown; **spathe** erect, ca. 12.5–13 cm long, apex not known; spathe tube deeply purple-tinged on outer surface, dark purple on inner surface, 6.5–7 cm \times 7 mm, drying matte, dark reddish brown on outer surface, weakly glossy on inner surface; spathe blade greenish cream, weakly purple-tinged, narrowly and most prominently so along outer margin toward base, ca. 6 cm \times 7 mm, drying matte, dark brown on outer surface, semiglossy on inner surface, marcescent, erect after anthesis; **spadix** erect, 11.5–12 cm long, sessile, adnate to

spathe 4.5–5 cm at base, ca. 1 cm less than total length of pistillate portion; pistillate portion 5.5–6 cm \times ca. 4 mm, drying medium-dark to dark reddish brown; fertile staminate portion ca. 5 cm \times 4–5 mm, narrowly rounded at apex, ellipsoid, drying dark reddish brown; sterile staminate portion ca. 1.5–1.8 cm \times 4 mm, cylindrical, drying dark blackish brown; pistils weakly coherent, 4 across the axis (viewed from above), ca. 2 mm long; ovary subglobose, ca. 1 \times 2–2.5 mm, drying tan; style Type 9 (Fig. 1), 0.8–1 \times 1.5–2.5 mm, weakly broader than ovary apex, the margins weakly coherent with those of adjacent styles; **stigma** 0.3–0.5 mm diam., elevated on and weakly wider than narrowed portion of style, drying medium to dark brown; synandria ca. 1 mm long, 2–2.2 \times 1 mm diam. and elongated in direction of axis, coherent, truncate, irregularly (4)5- to 6-lobed, (4)5- to 6-androus (mostly 5); sterile flowers 1–1.5 mm long, 0.5–1 \times 2.5–3 mm diam. and markedly elongated in direction of axis, in 7 whorls, deeply, irregularly lobed, coherent, truncate at apex and abruptly narrowing below in apical 2 whorls, otherwise 1- to 6-branched, the branches broadest and obtusely truncate at apex, narrowing below. Berries not known.

Phenology. Flowering is only known to occur in *Chlorospatha ricaurtensis* during the month of March.

Discussion. *Chlorospatha ricaurtensis* is known only from the type collection made at La Planada Reserve on the western slopes of the Cordillera Occidental in Nariño Department, Colombia, near the border with Ecuador, at 1800–1850 m elevation. The species would be expected to occur elsewhere in the department and southward into Ecuador, possibly northward into Cauca Department. *Chlorospatha ricaurtensis* is terrestrial and was collected in a pasture, and although nothing is known about the surrounding forest or its condition, it is possibly either lower montane wet forest or lower montane moist forest.

Chlorospatha ricaurtensis is a member of *Chlorospatha* sect. *Occidentales* and is distinguished by its sagittate, semiglossy, dark green leaf blades with the midrib and major venation paler on both surfaces, and the posterior lobes narrow and almost as long as the anterior lobe. The species is also distinguished by its purple-tinged petiole that is sheathed two thirds of its length, with the sheath free-ending, and large inflorescence (to 13 cm long) with the spathe tube deeply purple-tinged on the outer surface and dark purple on the inner surface, and the blade purple-tinged, greenish cream. The 5- to 6-androus synandria are unusual. The sterile staminate portion

of the spadix is unusually long, 1.5–1.8 cm, with most sterile flowers several-branched and densely arranged.

Chlorospatha ricaurtensis could be most easily confused with *C. planadensis*, with which it is sympatric at La Planada Reserve (see discussion under *C. planadensis*).

Chlorospatha ricaurtensis could possibly be confused with two species from Valle Department, in the vicinity of Calí, on the eastern and western slopes of the Cordillera Occidental at similar elevations: *C. giraldoi* and *C. noramurphyae* (see discussions under these two species).

60. *Chlorospatha risaraldensis* Croat & L. P. Hannon, sp. nov. TYPE: Colombia. Risaralda: Mpio. Mistrató, Jequadas distr., W slope of Cordillera Occidental, 1500 m, 5°26'N, 76°02'W, 28 Mar.–2 Apr. 1992, J. Betancur, J. Fernández, O. Rangel, S. Rentería & J. Guzmán 3287 (holotype, COL-35208!; isotype, COL-353379!). Figure 44B, C.

Herba hemiepiphytica. Petiolus 62.5–65 cm longus, vaginatus per 30–40 cm; lamina foliaris profunde 3-lobulata vel fere trisecta, 30–33 \times 32–38 cm, lobo medio elliptico, 26–31.5 \times 9–11(–14) cm, anguste confluyente cum lobo laterali, nervis primariis lateralibus utroque 8 ad 11. Inflorescentiae 3 in quaque axilla; pedunculus 35–40 cm \times 1–2 mm; spatha erecta, ca. 4.5 cm longa, tubo ca. 3.5 mm diam., lamina ca. 1.9 cm \times 3–4.5 mm diam.; spadix ca. 4.2 cm longus.

Hemiepiphytic herb; stem and internodes not known (all measurements made from dried material); cataphylls known only from fragments, drying glossy, pale tan, weakly fibrous, the fibers linear, paler than surface. LEAVES 2; **petioles** 62.5–65 cm long, glabrous, drying matte to weakly glossy, dark blackish brown, sheathed 30–40 cm, 1/2 to 2/3 of total length; sheath decurrent at apex; free portion 3–4 mm diam. midway; **blades** deeply 3-lobed to nearly trisect, 30–33 \times 32–38 cm, ca. 1.1 times wider than long, drying thin to thinly coriaceous, moderately bicolorous; upper surface drying weakly glossy, dark brown; lower surface drying weakly glossy to semiglossy; **medial lobe** \pm elliptical, 26–31.5 \times 9–11(–14) cm, (2.3 to)2.9 times longer than wide, acuminate at apex, usually as long as and narrower than lateral lobes, acute to cuneate and narrowly attached at base, 2.5–3 cm wide at point of attachment, weakly to moderately inequilateral, one side to 1.4 times wider than opposite side; **lateral lobes** directed toward the apex, 23–31.5 \times 10–12.5 cm, 2.3 to 2.8 times longer than wide, acute to acuminate at apex, broadest near base, markedly

inequilateral, the inner side always narrower, attenuate to long-attenuate toward base, narrowly confluent with medial lobe, the confluent portion 2–2.5 mm wide; outer side 4 to 7 times wider than inner side midway, broadly rounded at base, occasionally weakly constricted near base, moderately narrowly to briefly attenuate onto posterior rib; midrib and major veins drying \pm flattened on lower surface, conspicuously darker than surface, usually almost black; midrib round-raised on lower surface; posterior rib naked 2.5–5 cm per side; primary lateral veins on medial lobe 6 to 8 pairs, arising at 25° – 30° (-40°), straight to weakly arcuate, convex on lower surface; primary lateral veins on lateral lobes 8 to 11 pairs, 1 to 2 basal pairs fused near base, arising at 35° – 75° , weakly to markedly arcuate, aggregated toward base; secondary veins drying raised on lower surface, conspicuously darker than surface; tertiary veins drying in part prominulous, otherwise flat and visible on lower surface, moderately darker than surface; reticulate veins drying flat on lower surface, in part darker than surface; collective veins 3, the innermost arising from lowermost lateral vein at base, loop-connected with all preceding lateral veins, weakly scalloped, 2–8 mm from margin. INFLORESCENCES erect, to 3 per axil; peduncle held within the sheath, 35–40 cm \times 1–2 mm, glabrous, drying matte, dark blackish brown; **spathe** erect, entirely yellow-green, ca. 4.5 cm long, abruptly acuminate at apex, drying dark blackish brown; spathe tube ca. 2.5 cm \times ca. 3.5 mm; spathe blade ca. 1.9 cm \times 3–4.5 mm; **spadix** erect, ca. 4.2 cm long, sessile, adnate to spathe ca. 2 cm at base, the entire length of pistillate portion; pistillate portion ca. 2 cm \times ca. 2.5 mm; fertile staminate portion white, ca. 1.3 cm \times 3 mm, narrowly rounded at apex, \pm cylindrical, drying dark brown; sterile staminate portion 7–9 \times ca. 2 mm, drying tan; pistils weakly coherent, ca. 4 across the axis (viewed from above), ca. 0.5 mm long; ovaries subglobose, ca. 1–1.2 mm diam., drying medium brown; style Type 3 (Fig. 1), ca. 1 mm diam., weakly broader than ovary apex, the margins not coherent with those of adjacent styles; **stigma** ca. 0.3 mm diam., sessile, drying dark brown; synandria ca. 0.7 \times ca. 1 mm, coherent, truncate, deeply 3- to 4-lobed, 3- to 4-androus; sterile flowers ca. 0.5 mm long, 1–1.3 \times 0.5 mm diam. and elongated in direction of axis, coherent, truncate, subprismatic, in 5 to 6 whorls, drying tan. INFRUCTESCENCE (immature) 5.5 cm \times 7 mm; berries 2–2.5 mm diam.

Phenology. Flowering and fruiting are only known to occur in *Chlorospatha risaraldensis* during the months of March and April.

Etymology. *Chlorospatha risaraldensis* is named for Risaralda Department, Colombia, where this species is endemic.

Discussion. *Chlorospatha risaraldensis* is known only from the region of Mistrató in Risaralda Department, Colombia, in tropical rainforest on the western slopes of the Cordillera Occidental at 1500–1550 m elevation. The species would be expected to occur elsewhere within the department, also in Antioquia to the north and Valle to the south.

Chlorospatha risaraldensis is a member of *Chlorospatha* sect. *Chlorospatha* and is distinguished by its hemiepiphytic habit and deeply 3-lobed to nearly trisect leaf blades with the lateral lobes broader than and as long as the medial lobe or nearly so. The blades dry blackened, dark brown, with the midrib, major, and secondary venation almost black on the lower surface, as is the petiole. Also noteworthy are the numerous primary lateral veins on the lateral lobes (eight to 11 pairs), with most aggregated toward the base. The species is also distinguished by its small inflorescence (less than 5 cm long) and long peduncle (35–40 cm long).

Chlorospatha risaraldensis could not be easily confused with any species. Only *C. corrugata* shares its unusual blade shape and will be considered here (see discussion under *C. corrugata*). *J. Fernández et al.* 9745 has lateral lobes slightly shorter than the medial lobe and only weakly wider. It is a sterile specimen, but the label notes report details of the inflorescence that accord with this species and also indicate that the collection was hemiepiphytic. A fertile specimen was not found.

Paratype. COLOMBIA. **Risaralda:** Mpio. Mistrató, betw. Geguadas & Puerto de Oro districts, Pisones forest, 1550 m, $5^{\circ}26'N$, $76^{\circ}2'W$, 2 Apr. 1992, *J. Fernández et al.* 9745 (MO, QCNE).

61. *Chlorospatha sagittata* Croat & L. P. Hannon, sp. nov. TYPE: Ecuador. Imbabura: along Selva Alegre–Otavalo rd., 61.3 km S of jct. with main rd. at Otavalo, 1678 m, $0^{\circ}17'57''N$, $78^{\circ}30'08''W$, 1 May 2003, *Croat & L. P. Hannon* 88410 (holotype, MO-5687884–85!; isotypes, K!, QCNE!). Figure 45A–D.

Herba parum plus quam 1 m; internodia 1.5–2 \times 1–2.5 cm. Petiolus 59–105 longus, vaginatus per ca. 89 cm; lamina foliaris sagittata, 35–51 \times 22–34 cm, lobis posterioribus 16–25 \times 8.5–15 cm, nervis basalibus utroque 4 vel 5, nervis primariis lateralibus utroque 6 vel 7. Inflorescentiae 6 in quaque axilla; pedunculus usque ad 88 cm \times 5 \times 3 mm; spatha erecta, ca. 10.5 cm longa, tubo ca. 8 mm diam.; spadix ca. 8.2 cm longus.

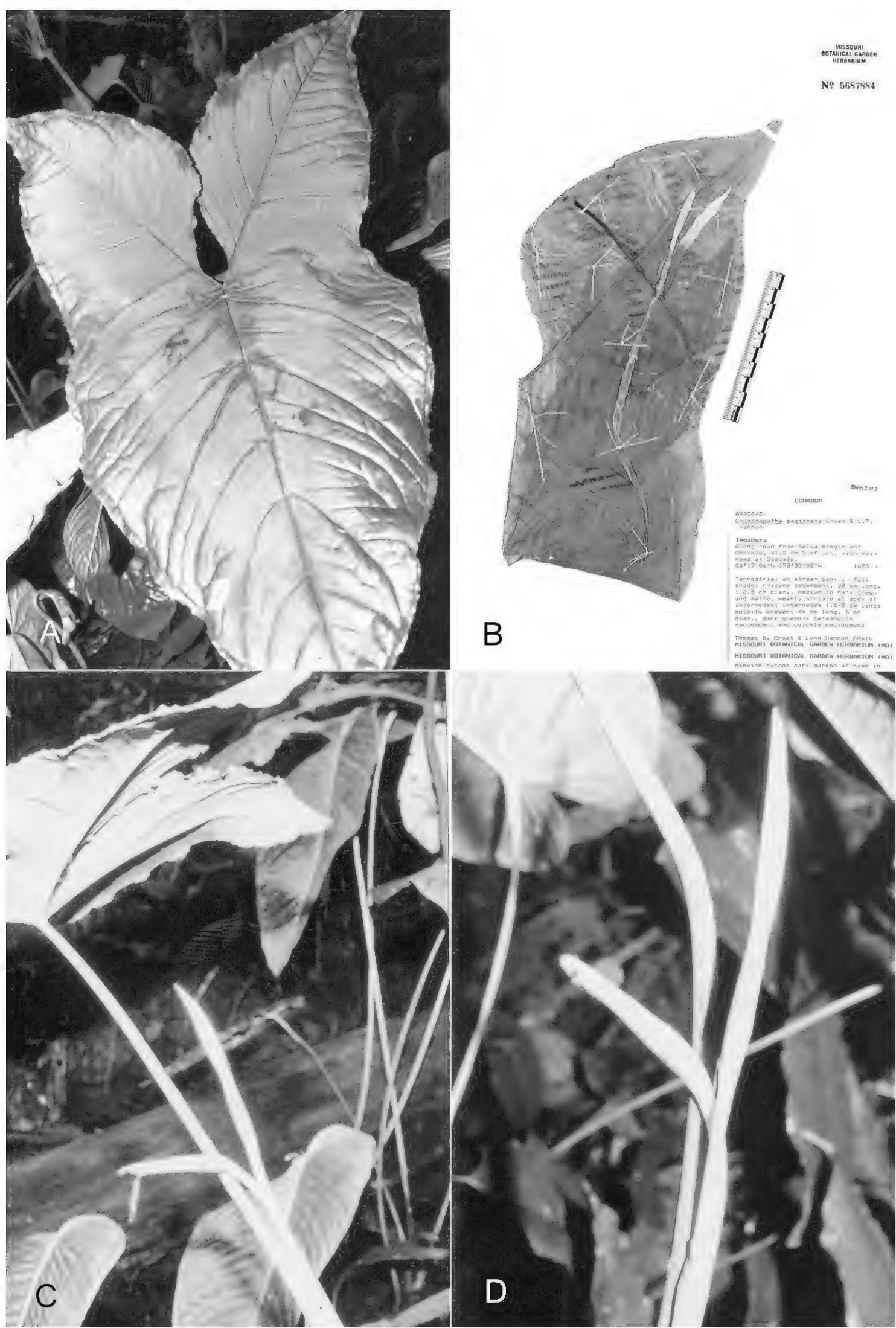


Figure 45. *Chlorospatha sagittata* Croat & L. P. Hannon. —A. Leaf blade adaxial surface. —B. Holotype sheet 2 of 2 (MO-5687884 [sheet 1 is MO-5687885, not pictured here]). —C. Fertile habit. —D. Sympodium, with three spathes of inflorescences near anthesis. A, C, D photographed from the holotype *Croat & L. P. Hannon 88410* (MO).

Terrestrial herb, on stream bank, slightly more than 1 m tall; stem decumbent, to 38 cm long, erect 15 cm, producing few bulbils randomly along its length; bulbils ovoid, green, 4×6 mm; internodes $1.5\text{--}2 \times 1\text{--}2.5$ cm, matte, medium-dark green, weakly striate at apex, drying 1–1.2 cm diam., matte, dark brown; cataphylls ultimately deciduous (total length and features not known), drying weakly glossy, dark brown. LEAVES 1 to 2, erect-spreading; **petioles** 59–105 cm long, moderately firm, glabrous, minutely many-ribbed throughout, matte, dark green, dark purple-mottled in narrow transverse bands, less so toward apex, drying matte to weakly glossy, dark reddish brown, sheathed 89 cm, more than $3/4$ of total length when in flower (less than $1/3$ on foliage leaf); sheath free-ending at apex, with one margin longer and more prominently rounded at apex than opposite margin; free portion 1–1.3 cm diam. midway, obtusely flattened toward apex, otherwise terete; **blades** sagittate, $35\text{--}51 \times 22\text{--}34$ cm, 1.5 to 1.6 times longer than wide, acuminate at apex, broadest at base, 1.2 times wider at base than across anterior lobe (measured tip to tip across posterior lobes), thinly coriaceous, moderately bicolorous, moderately constricted on one side in area of petiole attachment, weakly constricted on opposite side, drying thin, weakly to moderately bicolorous; upper surface broadly quilted, velvety, dark green, drying matte to weakly glossy, dark olive-green; lower surface weakly glossy to semiglossy, drying semiglossy to glossy; anterior lobe $23.5\text{--}35 \times 16\text{--}26.6$ cm, 1.3 to 1.5 times longer than wide, 1.4 to 1.5 times longer than posterior lobes, broadest below middle, \pm symmetrical; posterior lobes directed toward the base, $16\text{--}25 \times 8.5\text{--}15$ cm, 1.7 to 1.9 times longer than wide, broadly acuminate (or not) and acute to narrowly rounded at apex, broadest below middle, weakly inequilateral, the inner side narrower, weakly rounded at base, briefly attenuate onto posterior rib; midrib deeply sunken and concolorous on upper surface, round-raised and minutely ribbed on lower surface, weakly paler than surface, drying weakly raised and \pm flattened, weakly paler than surface; **basal veins** 4 to 5 pairs, coalesced into a prominent posterior rib; posterior rib naked 2–5 mm per side, round-raised, acutely 1-ribbed medially toward base; primary lateral veins 6 to 7 pairs, arising at $45^\circ\text{--}60^\circ$, \pm straight to weakly arcuate, quilted-sunken on upper surface, round-raised on lower surface, obtusely angular, minutely ribbed and concolorous, drying weakly raised and \pm flattened, concolorous to weakly paler than surface; secondary veins etched-sunken on upper surface, raised and concolorous on lower surface, drying weakly raised, concolorous to

weakly darker than surface; tertiary veins prominulous on lower surface, concolorous, drying weakly prominulous, weakly darker than surface; reticulate veins in part visible on lower surface, drying visible, in part weakly darker than surface, otherwise concolorous; collective veins 3, the innermost arising from the lowermost lateral vein on inner side of posterior lobe, \pm parallel to and 3–6 mm from margin. INFLORESCENCES erect, 6 per axil; peduncle held within the sheath, to 88 cm long, thicker than broad, 5 mm thick, 3 mm wide, matte, pale green, drying matte to semiglossy, medium yellowish brown; **spathe** erect, 10.5 cm long, lanceolate, acuminate at apex; spathe tube matte, medium green, deeply purple-tinged, most deeply so along outer margin and at base on outer surface, weakly glossy, dark purple on inner surface, $4.5 \text{ cm} \times 8 \text{ mm}$, drying matte, dark brown and weakly purplish on both surfaces; spathe blade matte, creamy white on both surfaces, $6 \text{ cm} \times 8 \text{ mm}$, drying matte, brownish green-cream on both surfaces, darker toward base, marcescent, erect after anthesis; **spadix** erect, 8.2 cm long, sessile, adnate to spathe 1.5 cm at base, slightly more than $1/2$ of the length of pistillate portion; axis medium maroon; pistillate portion maroon, $2.4\text{--}2.6 \text{ cm} \times 5 \text{ mm}$, weakly broadest midway, drying medium purplish brown; fertile staminate portion yellowish cream, $3.5 \text{ cm} \times 6.5 \text{ mm}$ midway, 4 mm diam. at base, \pm clavate, bluntly rounded at apex, drying brownish cream; sterile staminate portion pale pink, $1.8\text{--}2 \text{ cm} \times 4\text{--}5 \text{ mm}$, broadest at base, drying cream-colored; pistils laxly arranged, ca. 4 across the axis (viewed from above), ca. 2 mm long; ovaries densely, minutely dark maroon-speckled, obtusely conical, $1.3\text{--}1.5 \times 2\text{--}3$ mm, 3-locular, with pseudoaxile placentation, 8 to 10 ovules per locule; ovules small, hemianatropous, biseriate; funicles shorter than or as long as ovules; style Type 4 (Fig. 1), pinkish, $0.2 \times 2\text{--}2.5$ mm, moderately broader than ovary apex, obscurely attenuate, some margins weakly coherent with those of adjacent styles; **stigma** yellowish cream, $0.2\text{--}0.3 \times 0.6\text{--}0.8$ mm, obscurely elevated on style, appearing sessile, disklike, broadest and obtusely truncate at apex; synandria $1\text{--}2 \times 1.8\text{--}2$ mm, coherent, truncate, (3)4- to 6-lobed, mostly 4- to 6-androus; sterile flowers entirely pale pink in apical whorls, dark maroon at base in basal whorls, $0.5\text{--}0.8 \times 1.5\text{--}2$ mm, subprismatic or weakly lobed, truncate at apex or occasionally weakly broadly concave, \pm laxly arranged in basal whorls, weakly coherent in apical whorls, in 6 to 7 whorls. Berries not known.

Phenology. Flowering is only known to occur in *Chlorospatha sagittata* during the months of April

and May. Inflorescences emerge in slow progression, with several days between anthesis of one inflorescence and emergence of the next inflorescence at the apex of the petiole sheath.

Etymology. The epithet is taken from the Latin “sagittatus,” meaning “sagittate,” referring to the arrowhead shape of the leaf blade of *Chlorospatha sagittata*, with the posterior lobes directed toward the base.

Discussion. *Chlorospatha sagittata* is known only from the type locality in Imbabura Province, near the border with Pichincha, in lower montane wet forest on the western slopes of the Andes at 1678 m elevation. The species was collected on a stream bank in deep shade. It would be expected to occur elsewhere within both provinces and possibly northward into Carchi Province. The species is a member of *Chlorospatha* sect. *Occidentales* and is distinguished by its sagittate, velvety, dark green leaf blades and unusually long (105 cm long), purple-mottled petiole sheathed more than three fourths of its length, with the sheath free-ending at the apex. The peduncle is the longest recorded for the genus (to 88 cm long). The inflorescence is distinctive in having the spathe tube purplish, the ovaries and the axis of the spadix dark maroon, and the styles and sterile flowers pale pink. The style is unusual, of a type observed in only one species, but which possibly occurs in two other species. The mantle portion is broadly spreading, as in the other three species, yet obscurely attenuated, with the stigma appearing to be sessile, as in *C. hastata* and possibly also in *C. castula* and *C. corrugata*. The other species differ from *C. sagittata* in most respects and could not be confused with this species. The style is remarkably thin in the other species and somewhat more thickened in *C. sagittata*.

Chlorospatha sagittata could possibly be confused with *C. bayae* and *C. jaramilloi* from the western slopes of the Andes, with the latter known only from the western slopes of the Andes in Pichincha Province, Ecuador, and *C. bayae* known only from Valle Department in northern Colombia (see discussions under the latter two species).

62. *Chlorospatha sizemoreae* Croat & L. P. Hannon, sp. nov. TYPE: Ecuador. Zamora-Chinipe: Río Nangaritza, 45 min. by boat, upriver from end of rd. at Las Orquídeas, at base of cliffs above river, 1200–2000 m (est.), 4°16'42"S, 78°38'55"W, 19 Jan. 2004, *M. Sizemore 04-003* (holotype, MO-5882513!). Figures 46B, 47A–D.

Herba ca. 40 cm; internodia 0.5–1 × 1.5–2 cm; cataphylla 7–22 cm longa. Petiolus 26–35 cm longus, vaginatus per ca. 3.5–4 cm; lamina foliaris ± oblongo-elliptica, sagittata, 27.5–31.5 × 8–9.3 cm, lobis posterioribus 6–9 × 2.5–3.5 cm, nervis basalibus utroque 4 vel 5, nervis primariis lateralibus utroque 4; inflorescentiae 5 in quaque axilla; pedunculus 6.5–9.5 cm × 2.5 mm; spatha erecta, 4.3–5.6 cm, tubo 4–5 mm diam. (ante anthesin), lamina 2.5–3.1 cm longa; spadix 3.3–4.1 cm longus.

Terrestrial herb, ca. 40 cm tall; stem decumbent, erect 5 cm, with remnants of old cataphylls persisting intact at upper nodes; sap milky; internodes 0.5–1 × ca. 1.5–2 cm, weakly glossy to semiglossy, medium-dark green; cataphylls one to two, 7–22 cm long, obtuse with acumen at apex, acutely 1-ribbed abaxially in apical 3 cm, matte to weakly glossy, medium pink on outer surface, green-tinged in basal 1/4, densely irregularly weakly darker purple-lineate in narrow transverse bands, prominently so in apical 1/2, glossy and paler on inner surface, drying matte to weakly glossy, dark brown. LEAVES 4 to 5, erect-spreading; **petioles** 26–35 cm long, glossy, medium green, densely and weakly darker purple-lineate and purple-speckled in transverse bands, obscurely so in apical 3–4 cm, drying weakly glossy to semiglossy, dark brown, with epidermis in part separated ± intact and paler, sheathed ca. 3.5–4 cm, ca. 1/10 of total length; sheath weakly free-ending at apex, the sides convolute; free portion 5–6 mm diam. midway, terete, obtusely D-shaped in apical 1/4; **blades** ± oblong-elliptic, sagittate (subhastate on juvenile blade), frequently subhastate on drying, 27.5–31.5 × 8–9.3 cm (21 × 13 cm on juvenile blade), ca. 3.3 times longer than wide, weakly long-acuminate at apex, weakly broadest across anterior lobe, moderately constricted in area of petiole attachment, subcoriaceous, moderately bicolorous, drying thinly coriaceous; upper surface quilted, matte to weakly glossy, medium-dark grayish green, narrowly darker along midrib and major veins, drying matte, in part weakly glossy, medium-dark yellow-green; lower surface semiglossy to glossy, medium yellow-green, narrowly minutely colliculate along all veins, drying glossy, concolorous, narrowly paler along all veins; anterior lobe 23–25.5 × 8–9.3 cm (14 × 6.8 cm on juvenile blade), 2.7 times longer than wide, 2.9 to 3 times longer than posterior lobes, broadest near base, ± symmetrical to weakly inequilateral; posterior lobes directed toward the base, 6–9 × 2.5–3.5 cm, 2.4 to 3 times longer than wide, narrowly rounded at apex, broadest at base, moderately inequilateral, the inner side narrower, ± acute to weakly rounded at base, decurrent onto petiole; outer side 1.8 to 2.1 times wider than inner side midway; all venation drying etched-sunken on upper surface, concolorous;

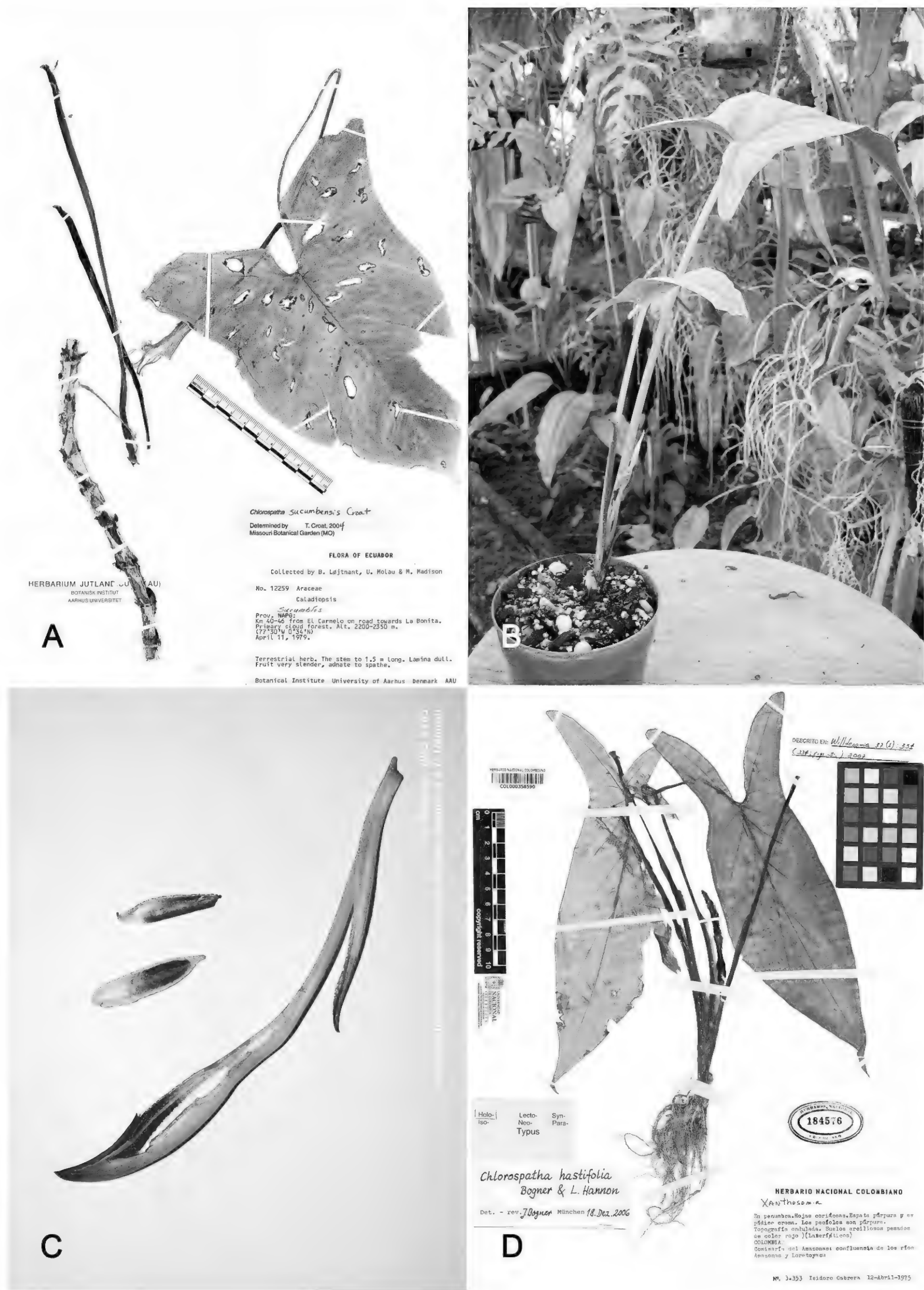


Figure 46. —A. *Chlorospatha sucumbensis* Croat & L. P. Hannon, the holotype Løjtnant et al. 12259 (AAP). —B. *Chlorospatha sizemoreae* Croat & L. P. Hannon, fertile plant habit from cultivar at Lynn Hannon greenhouse from the type collection Sizemore 04-003 (pre-anthesis; MO). —C. *Chlorospatha feuersteiniae* (Croat & Bogner) Bogner & L. P. Hannon, spathe cut open. —D. *Chlorospatha hastifolia* Bogner & L. P. Hannon, holotype Cabrera 3353 (COL-184576). Herbarium scan used by permission of COL.



Figure 47. *Chlorospatha sizemoreae* Croat & L. P. Hannon. —A. Leaf blade adaxial surface. —B. Stem showing a sympodium of successive inflorescences. —C. Close-up of inflorescence at anthesis, frontal view. —D. Close-up of inflorescence at anthesis, side view. Photos from the MO cultivar of the type collection *Sizemore 04-003*.

midrib and major veins deeply quilted-sunken on upper surface, convex on lower surface, concolorous to weakly paler than the surface, drying weakly raised, moderately darker than surface; midrib moderately paler yellow-green on upper surface; **basal veins** 4 to 5 coalesced into prominent posterior rib, the first free to the base or briefly fused 1–2 mm, extending into anterior lobe, 2 to 3 acroscopic, 1 to 2 basisopic; posterior rib acutely raised on lower surface, concolorous; primary lateral veins 4 pairs, arising at 25°–30°, straight to weakly arcuate, moderately darker than upper surface; secondary veins quilted-sunken on upper surface, less prominently so than major veins, weakly darker than surface, in part prominulous and otherwise flat on lower surface, concolorous, drying in part weakly darker than surface; tertiary and reticulate veins etched-sunken and concolorous on upper surface, visible on lower surface, flat, concolorous, drying flat and moderately paler than surface; collective veins 2 or 3, the innermost arising from apex of posterior rib, loop-connected with all preceding lateral veins, \pm parallel to and 3–5 mm from margin. **INFLORESCENCES** erect, 5 per axil, with a sweet, fruity fragrance at anthesis; peduncle held within the sheath, 6.5–9.5 cm \times 2.5 mm, obtusely triangular or cylindroid, semiglossy, pale-medium green, weakly darker-speckled in narrow transverse bands; **spathe** erect, 4.3–5.6 cm \times 4–5 mm (pre-anthesis), \pm cylindrical, prominently acuminate at apex, weakly constricted between tube and blade, ca. 1.5 cm wide (flattened) and \pm ovate, constricted between tube and blade and \pm funnel-shaped at anthesis, opening slightly more than 2/3 of total length; spathe tube matte, medium yellow-green on outer surface, glossy on inner surface, 1.7–2.5 cm \times ca. 7.5 mm at anthesis; spathe blade matte, much paler medium and yellow-green on both surfaces, with weakly darker longitudinal veins on outer surface, 2.5–3.1 cm long, erect-spreading and opening \pm broadly at anthesis, prominently acuminate at apex, the opening \pm elliptical, ca. 1.3 cm wide, with margins directed \pm forward, in-rolled in apical 7 mm, marcescent, erect after anthesis; **spadix** erect, 3.3–4.1 cm long, sessile, adnate to spathe 0.7–1.1 cm at base, ca. 2/3 of the length of pistillate portion; pistillate portion medium yellow-green, 1.4–1.7 cm \times 3.5 mm, broader than thick, broadest midway; fertile staminate portion matte, pale greenish yellow, 1.5–1.7 cm \times 2.5–3 mm, broadest near base, weakly tapering, narrowly rounded at apex; sterile staminate portion matte, greenish white, 5–6 \times 2–2.5 mm, broadest at base; pistils weakly coherent, 4 to 5 across the axis (viewed from above), ca. 2 mm long; ovaries \pm ovoid, glossy,

pale-medium yellow-green, ca. 1.5 \times 1 mm, broadest ca. midway, 2- to 3-locular, with pseudoaxile placentation; ovules 12 to 14 per locule, anatropous, biseriate; funicle shorter than ovule; style (Type 2, Fig. 1), ca. 0.5 mm long, comprising ca. 1/4 of the length of pistil, narrower than ovary apex, red chromoplasts lacking, the margins obscure, not coherent with those of adjacent styles; **stigma** greenish, ca. 0.2 mm diam., \pm cylindrical, weakly elevated on style; synandria ca. 1 \times 1–1.2 mm, truncate at apex, 2- to 3-lobed, 2- to 3-androus (mostly 3); sterile flowers 0.5–1 \times ca. 1.2 mm, frequently weakly elongated in direction of axis, coherent, truncate, subprismatic, in 4 whorls. Berries not known.

Phenology. Flowering in *Chlorospatha sizemoreae* is known only from a single flowering event in cultivation in the month of May. The species was collected in sterile condition in January. Several inflorescences emerge from the apex of the petiole sheath in quick succession before anthesis of the first, with seven to eight days between anthesis of one inflorescence and anthesis of the next.

Etymology. *Chlorospatha sizemoreae* is named for Mary Sizemore, who collected the species in 2004 and originally brought it to our attention and provided the material for the type.

Discussion. *Chlorospatha sizemoreae* is a member of *Chlorospatha* sect. *Orientalis* and is known only from the type collection made on the eastern slopes of the Andes in Zamora-Chinchipe Province, Ecuador, at the base of some cliffs along the Río Nangaritza on the western slopes of the Cordillera del Condor, at an estimated elevation of 1200–2000 m (based on GPS coordinates), in either premontane wet forest or lower montane wet forest, depending on actual elevation. The species possibly occurs in Peru, the collection site being near the Peruvian border; however, the mountain range possibly serves as an obstacle to distribution eastward into Peru. *Chlorospatha sizemoreae* is distinguished by its subcoriaceous, narrowly sagittate, grayish green leaf blades that are prominently quilted on the upper surface, with the tertiary and reticulate veins etched-sunken on that surface. The species is also distinguished by its short, narrow posterior lobes. The lower surface of the blade is narrowly colliculate along all veins, a character frequently observed in species from the Amazon basin; however, in this species, the minor veins are flat and somewhat obscure, which is not the case in the other species, in all of which the lower blade surface is conspicuously reticulate, with the minor

veins more or less raised or prominulous. The species is also distinguished by its unusual, somewhat bottle-shaped pistils with briefly attenuated styles. It is one of only three species with attenuated styles in section *Orientales*, but it could not be confused with the other two species: *C. cutucuensis* and *C. portillae*.

Chlorospatha sizemoreae could not be confused with any other species, particularly any species from the eastern slopes of the Andes in Colombia or Ecuador. The shape of the leaf blade is similar to that of *C. longiloba* from the western slopes in Ecuador, both species having long, relatively narrow, oblong-elliptic, sagittate blades with short, narrow posterior lobes. However, the colliculate area bordering all veins on the lower surface in *C. sizemoreae* is lacking in *C. longiloba*. The inflorescence of the latter species is considerably larger, with the spathe tube and some portions of the blade more or less purple, whereas those of *C. sizemoreae* are yellow-green, lacking any purple. The style of the latter species lacks a mantle, whereas that of *C. longiloba* has a broadly spreading mantle.

Cultivated specimen examined. ECUADOR. **Zamora-Chinchipe:** Río Nangaritza, 1200–2000 m (est.), 4°16'42"S, 78°38'55"W, 19 Jan. 2004 (cultivated by Lynn Hannon), *M. Sizemore* 04-003.

63. *Chlorospatha stellasarreae* Croat & L. P. Hannon, sp. nov. TYPE: Colombia. Valle: Queremal, Campamento Tokio (telecom towers), ca. 9 km W of Queremal, 2000–2100 m, 3°30'N, 76°42'W, 21 Apr. 1989, *J. Luteyn, J. Giraldo & S. Sarrea* 12587 (holotype, MO-3789759!). Figure 44D.

Herba usque ad 20 cm; internodia (1–)2–4 cm × 5–7 mm; cataphylla 6.5–7.5 cm longa. Petiolus 8–10 cm longus, vaginatus per 5–9 cm; lamina foliaris ovata vel ovato-elliptica, (6.5–)8.8–9.9 × (3.3–)4.3–5.8 cm, rotundata vel debiliter subcordata vel cordulata ad basim, nervis primariis lateralibus utroque 4 vel 5(6). Inflorescentiae 2 vel 3 in quaque axilla; pedunculus 5.5–7 cm × < 1 mm; spatha erecta, 6–6.5 cm longa, tubo 2–3 mm diam., lamina 3–3.3 cm × ca. 4 mm; spadix ca. 5.2 cm longus.

Terrestrial herb, to 20 cm tall; stem decumbent, to 33.5 cm long, with remnants of old leaf bases persisting ± intact along its length (all measurements made from dried material); internodes (1–)2–4 cm × 5–7 mm, drying matte to weakly glossy, medium to medium-dark brown, irregularly transversely striate, the striations short; cataphylls ultimately deciduous, 6.5–7.5 cm long, obtuse with acumen at apex, obtusely 1-ribbed abaxially, drying weakly glossy to semiglossy, medium-dark reddish brown. LEAVES 3 to 7, erect-spreading; **petioles** 8–10 cm long,

glabrous, drying matte, dark reddish brown, sheathed 5–9 cm, most of length (2/3 in juvenile plants); sheath free-ending at apex; free portion ca. 1 mm diam. midway; **blades** ovate to ovate-elliptic, (6.5–)8.8–9.9 × (3.3–)4.3–5.8 cm, 1.7 to 1.9 times longer than wide, weakly acuminate at apex, broadest at or below middle, rounded to weakly subcordate or cordulate at base and inequilateral, decurrent onto petiole, weakly inequilateral, with one side 2–3 mm wider than opposite side, drying thinly coriaceous, weakly bicolorous; upper surface drying matte to weakly glossy, medium-dark to dark yellow-green; lower surface drying weakly glossy to semiglossy; midrib round-raised on lower surface, drying weakly raised to ± flattened, weakly darker than surface; primary lateral veins 4 to 5(6) pairs, arising at 30°–75°(–80°) (most at ca. 40°), most acutely toward apex, weakly arcuate, convex on lower surface, drying ± flattened, concolorous to weakly darker than surface; secondary veins drying weakly raised and ± concolorous on lower surface; tertiary veins drying in part weakly prominulous, otherwise flat and in part distinct on lower surface, ± concolorous; reticulate veins drying obscure; collective veins 3, the innermost arising from the base, loop-connected with all preceding lateral veins, ± parallel to and 3–6 mm from margin. INFLORESCENCES erect, 2 to 3 per axil; peduncle held within the sheath, 5.5–7 cm × < 1 mm, drying matte to weakly glossy, dark brown; **spathe** erect, pale green, 6–6.5 cm long, acuminate at apex; spathe tube 3–3.2 cm × 2–3 mm, drying matte to weakly glossy, dark brown on outer surface, weakly glossy and weakly paler on inner surface, densely pale, punctiform medially; spathe blade 3–3.3 cm × ca. 4 mm, drying weakly glossy, medium to dark brown on outer surface, semiglossy and weakly paler on inner surface, with reticulate venation conspicuous, prominulous and moderately darker than surface, marcescent, erect after anthesis; **spadix** erect, ca. 5.2 cm long, sessile, adnate to spathe 3–3.2 cm at base, the entire length of pistillate portion; pistillate portion 3–3.2 cm × ca. 1.5 mm, drying dark reddish brown; fertile staminate portion ca. 2 cm × 2 mm, bluntly acute at apex, ellipsoid, drying medium-dark reddish brown; sterile staminate portion ca. 2 × 1–1.5 mm, drying medium-dark reddish brown; pistils markedly laxly arranged, the axis bare between whorls, 1 to 2 across the axis (viewed from above), 1.5–1.75 mm long; ovaries ± cylindrical to obtusely conical, ca. 1 × 1.2–1.5 mm, drying pale tan with darker veins; style Type 7 (Fig. 1), ca. 0.5–0.75 × 0.3–0.5 mm, comprising slightly less than 1/2 of the length of pistil, narrower than ovary apex, the margins not coherent with those of adjacent styles; **stigma** ca.

0.3 mm diam., elevated on and weakly broader than narrowed portion of style; synandria ca. $0.8 \times 1\text{--}1.1$ mm, coherent, truncate, (2)3- to 4(5)-lobed, (2)3- to 4(5)-androus (mostly 4), with flowers lacking microsporangia in apical whorl; sterile flowers $0.5\text{--}0.7 \times$ ca. 0.8 mm, fungiform (like toadstools), broadest and weakly convex at apex, abruptly narrowing below, laxly arranged, in 1 to 2 whorls (extending briefly into pistillate and fertile staminate portions). Berries green.

Phenology. Flowering and fruiting are only known to occur in *Chlorospatha stellasarreae* during the month of April.

Etymology. *Chlorospatha stellasarreae* is named for Ing. Stella Sarrea, Director of Parque Nacional Faldas de Farrallones in Colombia, who, along with James Luteyn and Jorge Giraldo, participated in collecting the type specimen.

Discussion. *Chlorospatha stellasarreae* is known only from the type locality near the Tokio Microwave Station near Queremal in Valle Department, Colombia, at 2000–2100 m elevation in premontane wet forest on the western slopes of the Cordillera Occidental. The species was reported as locally abundant and would be expected to occur elsewhere within the department, although it should be noted that the area around Queremal exhibits a high level of endemism.

Chlorospatha stellasarreae is a member of *Chlorospatha* sect. *Occidentales* and could not be confused with any other species. It is the smallest known species of *Chlorospatha*, the small, ovate leaf blades making it unique in the genus. The blades dry yellow-green and are less than 10 cm long on fully mature specimens, and rounded to weakly subcordate at the base. The species is also distinguished by its long internodes (usually 2–4 cm long) and long-sheathed petiole, which is sheathed most of its length when in flower, with the sheath prominently free-ending at the apex. The spathe is entirely pale green and 6–6.5 cm long, relatively large for such a diminutive plant. No other species observed has so few pistils so laxly arranged. There are only one to two pistils per whorl and the axis is clearly visible and naked between the whorls. The sterile staminate portion of the spadix is also unusual, being only ca. 2 mm long, with only a few fungiform (like toadstools) flowers.

B. Løjtnant, U. Molau & M. Madison 12259 (holotype, AAU!). Figure 46A.

Herba usque ad 50 cm; internodia 2–2.5(–3) cm \times 8–10 mm. Petiolus ca. 33.5 cm longus, vaginatus per ca. 10.5 cm; lamina foliaris subhastata, ca. 21.5×17 cm, lobis posterioribus ca. 9.7×6.2 cm, nervis basalibus utroque 5 vel 6. Inflorescentiae 2 in quaque axilla; pedunculus 18–19 cm \times ca. 3 mm; spathae tubo ca. 3.7×4.5 mm; spadix (parte pistillata) ca. 3.5×3 mm.

Terrestrial herb, to 50 cm tall; stem decumbent, to 1.5 m long, with remnants of old cataphylls persisting as short, \pm intact fragments along its length (all measurements made from dried material); internodes 2–2.5(–3) cm \times 8–10 mm, drying matte, dark reddish brown, with epidermis in part separated and pale tan; cataphylls (known only from fragments) drying matte, dark brown. **LEAVES** 1; **petiole** 33.5 cm long, drying glabrous, matte to weakly glossy, medium-dark brown, paler and darker transversely lineate toward base, sheathed 10.5 cm, ca. 1/3 of total length; sheath free-ending at apex, drying paler on inner surface; free portion ca. 2 mm diam. midway; **blade** subhastate, 21.5×17 cm, briefly acuminate at apex, broadest at base, 1.3 times longer than wide, 1.3 times broader at base than across anterior lobe (measured tip to tip across posterior lobes), weakly concave in area of petiole attachment, drying thin, weakly bicolorous; upper surface drying matte, medium-dark olive-green; lower surface drying semi-glossy, medium green, narrowly colliculate along all veins except reticulate and some tertiary; anterior lobe 16×13 cm, 1.2 times longer than wide, 1.6 times longer than posterior lobes, broadest below middle, \pm symmetrical; posterior lobes 9.7×6.2 cm, 1.6 times longer than wide, narrowly rounded at apex, broadest at base, weakly inequilateral, the inner side narrower, acute to weakly rounded at base, decurrent onto petiole; outer side 1.5 to 1.7 times broader than inner side midway; all orders of venation drying visible on upper surface, weakly prominulous and weakly darker than surface; midrib, major, and secondary veins drying raised on lower surface, weakly granular-puberulent, weakly paler than surface; **basal veins** 5 to 6 pairs, coalesced into prominent posterior rib; primary lateral veins 5 to 7 pairs, arising at $55^\circ\text{--}65^\circ$, \pm straight to weakly arcuate, occasionally prominently arcuate; tertiary veins drying mostly raised on lower surface, weakly paler than surface, in part prominulous and weakly darker than surface; reticulate veins drying distinct and visible on lower surface, weakly darker than surface; collective veins 3, the innermost arising from lowermost lateral vein on inner side of posterior lobe, loop-connected with all preceding lateral veins, \pm

- 64. *Chlorospatha sucumbensis*** Croat & L. P. Hannon, sp. nov. TYPE: Ecuador. Sucumbíos: Km. 40–46 from El Carmelo on rd. to La Bonita, 2200–2350 m, $0^\circ 34'N$, $77^\circ 30'W$, 11 Apr. 1979,

parallel to and 7–9 mm from margin. INFLORESCENCES 2 per axil, erect-spreading; peduncle held within the sheath, 18–19 cm \times 3 mm, drying matte to weakly glossy, dark brown; **spathe** total length not known; spathe tube 3.7 cm \times 4.5 mm midway, drying matte, dark reddish brown, narrowly weakly paler along outer margin; spathe blade not known; **spadix** presumably erect, total length not known, sessile, adnate to spathe 3.5 cm at base, entire length of pistillate portion; pistillate portion 3.5 cm \times ca. 3 mm, weakly broadest midway, drying brownish yellow; fertile staminate portion not known; sterile staminate portion not known; pistils weakly coherent, more laxly arranged near base, ca. 3 across the axis (viewed from above), ca. 2 \times 1.5–2 mm; ovaries subglobose, ca. 2 mm diam.; style Type 9 (Fig. 1), 2–2.5 mm diam., briefly attenuate, weakly broader than ovary apex, the margins coherent with those of adjacent styles; **stigma** ca. 0.5 mm diam., disklike, elevated on style, drying medium reddish brown; synandria not known; sterile flowers not known. INFRUDESCENCE (immature) 5.5 cm \times 4.5 mm, drying matte, dark reddish brown; berries not known.

Phenology. Flowering and fruiting are only known to occur in *Chlorospatha sucumbensis* during the month of April.

Etymology. *Chlorospatha sucumbensis* is named for Sucumbíos Province, Ecuador, where the type was collected and the new species is endemic.

Discussion. *Chlorospatha sucumbensis* is known only from the type locality in lower montane wet forest in Sucumbíos Province, Ecuador, on the eastern slopes of the Andes at 2200–2350 m elevation, along the El Carmelo–La Bonita road that parallels the border with Colombia. The species would almost certainly occur in adjacent Carchi Province and in Putumayo Department, Colombia, directly across the border.

Chlorospatha sucumbensis is one of only two species in *Chlorospatha* sect. *Occidentales* that occur on the eastern slopes of the Andes, the other being *C. huilensis* (see discussion under *C. huilensis*).

65. *Chlorospatha timbiquensis* Croat & L. P. Hannon, sp. nov. TYPE: Colombia. Cauca: Timbiquí, 100 m (est.), 1903, *C. Lehmann* 390 (holotype, K!). Figure 48A.

Herba ca. 50 cm; internodia ca. 1 cm \times 5 mm; cataphylla usque ad 21 cm longa. Petiolus 20–30 cm longus, vaginatus per 12–22 cm; lamina foliaris hastata vel subhastata, 16.5–18 \times 12.7–14.3 cm, lobis posterioribus 6.3–9.5 \times 2.7–3.5 cm, nervis basalibus utroque 2, nervis primariis lateralibus

utroque 3 vel 4. Inflorescentiae 2 in quaque axilla; pedunculus 23–26 cm \times 1–1.5 mm; spatha erecta, ca. 8.5 cm longa, tubo ca. 3 mm diam., lamina ca. 5 cm \times 6 mm; spadix ca. 6.2 cm longus.

Terrestrial herb, ca. 50 cm tall; stem with remnants of old cataphylls persisting \pm intact along its length (all measurements made from dried material); internodes ca. 1 cm \times 5 mm, drying matte, dark brown; cataphylls to 21 cm long, cuspidate at apex, drying matte, dark brown. LEAVES 4, erect-spreading; **petioles** 20–30 cm long, drying glabrous, matte to weakly glossy, dark brown, sheathed 12–22 cm, more than 3/4 of total length (1/3 to 1/2 when sterile); sheath decurrent at apex; free portion 2–2.5 mm diam. midway, finely many-ribbed abaxially, possibly sulcate near apex; **blades** hastate to subhastate, 16.5–18 \times 12.7–14.3 cm, ca. 1.3 times longer than wide, acute to acuminate at apex (rarely long-acuminate), broadest at base, 1.3 to 1.9 times wider at base than across anterior lobe (measured tip to tip across posterior lobes), weakly constricted in area of petiole attachment, drying moderately thin, moderately bicolorous; upper surface drying matte to weakly glossy, dark brown; lower surface reticulate, drying weakly glossy; anterior lobe 13–14 \times (6.7–)9–10.2 cm, ca. 1.5 times longer than wide, 1.5 to 2.2 (to 3.3) times longer than posterior lobes, broadest below middle, weakly inequilateral; posterior lobes directed outward, 6.3–9.5 \times 2.7–3.5 cm, 2.1 to 3.2 (to 3.4) times longer than wide, bluntly acute to narrowly rounded at apex, broadest at base, moderately to markedly inequilateral, the inner side narrower, rounded toward base and decurrent onto petiole; outer side 2 to 3.3 times wider than inner side midway, \pm straight to weakly concave toward base; midrib, major, and secondary veins raised and granular-puberulent on lower surface, drying raised, darker than surface; midrib minutely ribbed on lower surface; **basal veins** 2 pairs, coalesced into prominent posterior rib; primary lateral veins 3 to 4 pairs, arising at 30°–40°, weakly arcuate, minutely many-ribbed on lower surface; tertiary veins granular-puberulent on lower surface, drying mostly weakly raised, otherwise prominulous, darker than surface; reticulate veins drying mostly prominulous, otherwise visible and flat on lower surface, darker than surface; collective veins 3, the innermost arising at apex of posterior rib, loop-connected with all preceding lateral veins, \pm parallel to and 4 mm from margin. INFLORESCENCES erect, 2 per axil; peduncle held within the sheath, 23–26 cm \times 1–1.5 mm, longer than petiole, drying matte, dark brown; **spathe** erect, 8.5 cm long, acute at apex; spathe tube 3.5 cm \times 3 mm, drying matte, dark brown; spathe blade ca. 5 cm \times 6 mm, drying matte, moderately paler than tube,

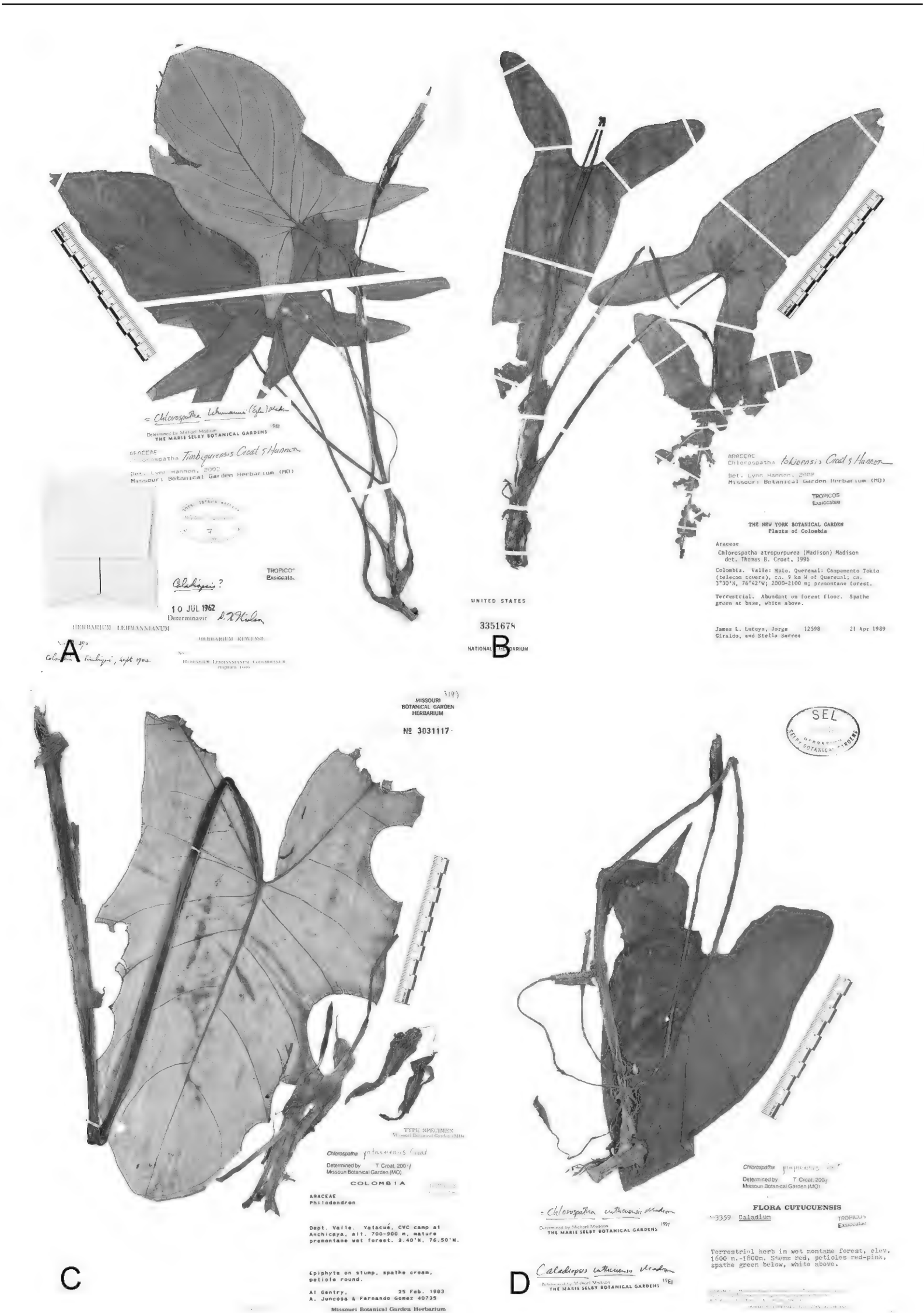


Figure 48. —A. *Chlorospatha timbiquensis* Croat & L. P. Hannon, *Lehmann* 390 (K holotype). —B. *Chlorospatha tokioensis* Croat & L. P. Hannon, the isotype *Luteyn et al.* 12598 (US-3351678). —C. *Chlorospatha yatacuensis* Croat & L. P. Hannon, the holotype *Gentry et al.* 40735 (MO-3031117). —D. *Chlorospatha yaupiensis* Croat & L. P. Hannon, the holotype *Madison et al.* 3359 (SEL-16544).

marcescent, erect after anthesis; **spadix** erect, 6.2 cm long, sessile, adnate to spathe 2 cm at base, most of the length of pistillate portion; pistillate portion 2.5 cm \times ca. 2 mm, drying creamy white; fertile staminate portion 3.1 cm \times ca. 3 mm, acute at apex, ellipsoid, drying medium dark brown; sterile staminate portion ca. 7 \times 1–1.5 mm, narrowest midway, naked in basal 1/3, drying dark brown; pistils weakly coherent, more laxly arranged near base, 3 to 4 across the axis (viewed from above), 1–1.5 mm long; ovaries subglobose, ca. 1.5 mm diam., drying creamy white with weakly darker veins; style Type 9 (Fig. 1), ca. 0.5 \times 1–1.3 mm, comprising ca. 1/4 to 1/3 of the length of pistil, broader than ovary apex, the margins \pm coherent with those of adjacent styles; **stigma** 0.3–0.5 mm diam., weakly elevated on narrowed portion of style, drying pale amber; synandria 1–1.5 \times 1–1.5 mm, weakly elongated in direction of axis in basal 3 whorls, coherent, truncate, 3- to 4(5)-lobed, 3- to 4(5)-androus; sterile flowers ca. 1 mm long, 0.8–0.9 \times 1.5 mm diam. and \pm elongated in direction of axis, subprismatic to subrounded, truncate, markedly laxly arranged, in 3 to 4 whorls. **INFRUCTESCENCE** (immature) 5 cm \times 6 mm, drying dark brown; berries ca. 2 mm diam., drying dark tan.

Phenology. Flowering and fruiting are only known to occur in *Chlorospatha timbiquensis* during the month of September.

Etymology. *Chlorospatha timbiquensis* is named for the town of Timbiquí on the Río Timbiquí in Cauca Department of Colombia, near which the type was collected.

Discussion. *Chlorospatha timbiquensis* is known only from the type, a Lehmann collection made in 1903, near the Pacific town of Timbiquí in Cauca Department, Colombia. The town is near the coast, near the mouth of the Río Timbiquí; therefore, the authors have estimated the elevation to be ca. 100 m and the life zone as tropical wet forest.

Chlorospatha timbiquensis is a member of *Chlorospatha* sect. *Occidentales* and is distinguished by its hastate to subhastate leaf blades with all abaxial venation drying raised or prominulous, relatively short yet narrow posterior lobes, and long petiole sheath and peduncle. The petiole is sheathed more than three fourths of its length and the peduncle is longer than the petiole, but the inflorescence is relatively small, less than 9 cm long. *Chlorospatha timbiquensis* is also distinguished by its style, which is briefly attenuated and dries creamy white, and the sterile staminate portion of the spadix, which is

markedly laxly flowered, with the axis naked in the basal one third.

Chlorospatha timbiquensis could not be easily confused with any species. Madison (1981) previously filed *Lehmann 390*, the type for *C. timbiquensis*, as *C. lehmannii*, but the collection differs from that species in significant ways and should be considered distinct. *Chlorospatha lehmannii* has leaf blades with proportionally longer posterior lobes, the posterior rib naked 5–7 mm on each side, all abaxial venation (except midrib) drying flattened, the petiole sheathed ca. one half of its length and the sheath free-ending at the apex. In *C. timbiquensis*, the posterior lobes are short, with the inner margins decurrent onto the petiole (posterior rib not naked); all abaxial venation dries raised or prominulous; the petiole is sheathed more than three fourths of its length; and the sheath is decurrent at the apex. In *C. lehmannii*, the peduncle is one half (two thirds) as long as the petiole and the spathe is more than 10 cm long, thus differing from *C. timbiquensis*, in which the peduncle is longer than the petiole and the spathe is less than 9 cm long. The style of *C. lehmannii* is long-attenuated and only as wide as the ovary apex, whereas that of *C. timbiquensis* is briefly attenuated and broader than the ovary apex. The sterile staminate portion of the spadix is markedly laxly flowered in the latter species, with the axis bare in the basal one third and the flowers subprismatic. That portion is densely flowered in *C. lehmannii* and the flowers are fungiform (like toadstools) or branched.

There are two specimens of *Lehmann 390* at Kew, and it is apparently a mixed collection. The leaf blade of the sterile specimen dries weakly or not at all bicolorous, with the upper surface weakly glossy to semiglossy, medium-dark brown, the lower surface semiglossy and smooth (not reticulate), and the anterior lobe narrowly oblong-elliptic, 4 times longer than wide, and long-acuminate at the apex. All abaxial venation is more or less flattened and paler than the surface. In the type indicated for *C. timbiquensis* (cf. Fig. 48A), which is a fertile specimen, the blade dries moderately bicolorous, with the upper surface matte to weakly glossy dark brown, the lower surface reticulate and weakly glossy, and the anterior lobe comparatively short, broad, and ovate, 1.5 times longer than wide and weakly to moderately acuminate at the apex, with the abaxial venation raised or prominulous and darker than the surface. The sterile specimen has been determined as *C. grayumii*, a new species from Chocó Department to the north of the type locality of *C. timbiquensis* from Cauca Department in Colombia and, therefore, has been assigned a new number, *Lehmann 390A* (K).

66. *Chlorospatha tokioensis* Croat & L. P. Hannon, sp. nov. TYPE: Colombia. Valle: Mpio. Quere-mal, Campamento Tokio (telecom towers), 9 km W of Quere-mal, 2000–2100 m, ca. 3°30'N, 76°42'W, 21 Apr. 1989, J. Luteyn, J. Giraldo & S. Sarrea 12598 (holotype, MO-3789758!; isotypes, NY!, US!). Figure 48B.

Herba ca. 50 cm; internodia 1–1.5 × 1–2 cm. Petiolus 24.5–44.5 cm longus, vaginatus per 8–13.5 cm; lamina foliaris subhastata, 21.5–34.5 × 14–27 cm, lobis posteri-oribus 9–12(–14.5) × 2.6–4(–6.2) cm, nervis basalibus utroque 5 ad 7(ad 9), nervis primariis lateralibus utroque 5 ad 6(7). Inflorescentiae 2 in quaque axilla; pedunculus 13.5–15 cm × 1–2 mm; spathe erecta, 8.8–9.5 cm longa, tubo 5–6 mm diam., lamina ca. 5 cm × 6–7 mm; spadix 6.6–8 cm longus.

Terrestrial herb, ca. 50 cm tall; stem decumbent, to 60 cm long, with remnants of old leaf bases and cataphylls persisting ± intact along its length (all measurements made from dried material); internodes 1–1.5 × 1–2 cm, drying matte, dark brown; cataphylls 9–11(–20) cm long, obtuse with acumen at apex (acumen to 4 mm long), drying weakly glossy, dark yellowish to reddish brown. LEAVES 2 to 3, erect-spreading; **petioles** 24.5–44.5 cm long, drying gla-brous, weakly glossy, pale-medium to dark brown, sheathed 8–13.5 cm, ca. 1/3 of total length; sheath decurrent at apex; free portion 2–3(–4) mm diam. midway; **blades** subhastate, 21.5–34.5 × 14–27 cm, 1 to 1.5 times longer than wide, acute to bluntly acute or weakly acuminate at apex, broadest at base, (2.2 to)2.5 to 3.5 times broader at base than across anterior lobe (measured tip to tip across posterior lobes), weakly to moderately constricted in area of petiole attachment, thin, drying weakly to moderately bicolorous; upper surface drying matte to weakly glossy, medium-dark to dark green or weakly brownish green, with pale, punctiform to short, linear raphid cells; lower surface drying weakly glossy to semiglossy; anterior lobe 14–25 × 5.5–7.7(–13) cm, (1.9 to)2.3 to 3.5 times longer than wide, (1.3 to)1.6 to 1.8 times longer than posterior lobes, broadest near base, ± symmetrical to weakly inequilateral; posterior lobes directed outward, 9–12(–14.5) × 2.6–4(–6.2) cm, (2.3 to)2.8 to 4 times longer than wide, bluntly acute to narrowly rounded at apex, broadest below middle, ± symmetrical to weakly inequilateral, the inner side weakly rounded toward base rarely broadly so, briefly attenuate onto posterior rib; outer side straight to weakly concave toward base; midrib round-raised on lower surface, drying raised, concolorous to weakly paler or weakly darker than surface, rarely much darker toward base; **basal veins** 5 to 7(9) pairs, coalesced into a prominent posterior rib; posterior rib naked 3–12 mm per side; primary lateral

veins 5 to 6(7) pairs, arising at 30°–55°, most acutely toward apex, moderately arcuate, occasionally irregu-larly ascending, rarely straight, round-raised on lower surface, drying ± raised, occasionally in part weakly flattened, concolorous to weakly paler than surface, occasionally weakly darker; secondary veins raised on lower surface, drying entirely or in part raised and otherwise prominulous, concolorous to weakly paler than surface; tertiary veins drying mostly prominulous on lower surface, otherwise visible and distinct, ± concolorous to weakly darker than surface; reticulate veins drying obscure; collective veins 3, the innermost arising from the lowermost lateral vein on inner side of posterior lobe, loop-connected with all preceding lateral veins, ± parallel to and 2–7 mm from margin. INFLORESCENCES erect, 2 per axil; peduncle held within the sheath, 13.5–15 cm × 1–2 mm, drying matte, medium to dark brown; **spathe** erect, 8.8–9.5 cm long, ± acute at apex; spathe tube green, 4–4.5 cm × 5–6 mm, drying matte, dark reddish brown on outer surface, weakly glossy, moderately paler on inner surface; spathe blade white, ca. 5 cm × 6–7 mm, drying weakly glossy, dark brown on outer surface, weakly glossier and concolorous on inner surface, marcescent, erect after anthesis; **spadix** erect, 6.6–8 cm long, sessile, adnate to spathe 3.8–4.5 cm at base, the entire length of pistillate portion; pistillate portion 3.8–4.5 cm × ca. 3 mm, drying dark purplish brown; fertile staminate portion 2.7–3.5 cm × 2–4.5 mm, narrowly rounded at apex, weakly clavate or ellipsoid, drying medium orangish brown or medium-dark grayish brown; sterile staminate portion 1–1.5 × ca. 2 mm, drying medium grayish brown; pistils weakly coherent, ca. 3 across the axis (viewed from above), ca. 2 mm long; ovaries subglobose, ca. 1.1 × ca. 2 mm, drying dark tan; style Type 8 (Fig. 1), ca. 0.8 × 1.3–1.8 mm, weakly broader than ovary apex, the margins ± coherent with those of adjacent styles; **stigma** 0.5–0.8 mm diam., moderately elevated on and broader than narrowed portion of style, drying medium reddish brown; synandria ca. 1 × 1.5–2 mm., coherent, truncate, 3- to 4(5)-lobed, 3- to 4(5)-androus (mostly 3); sterile flowers ca. 0.5–0.8 × 0.6–1 mm, fungiform (like toadstools) and convex at apex, or deeply lobed (as per synandria but lacking microsporangia), ± laxly arranged, in 1 to 2 whorls. Berries not known.

Phenology. Flowering is only known to occur in *Chlorospatha tokioensis* during the month of April.

Etymology. *Chlorospatha tokioensis* is named for Estación Micron-das Tokio, a telecommunications station in Valle Department of Colombia, where the new species is endemic.

Discussion. *Chlorospatha tokioensis* is known only from the type collection made near the Estación Microndas Tokio, an encampment with telecommunications towers near Queremal in Valle Department, Colombia, in premontane wet forest on the western slopes of the Cordillera Occidental at 2000–2100 m elevation. The species would be expected to occur elsewhere in the department.

Chlorospatha tokioensis is a member of *Chlorospatha* sect. *Occidentales* and is distinguished by its greenish drying, subhastate leaf blades with long, narrow posterior lobes. The petiole of *C. tokioensis* is sheathed one third of its length, and the peduncle is accordingly short, 13.5–15 cm. The inflorescence is of moderate size, 8.8–9.5 cm long, with the spathe tube green and the blade white. The unusually short, sterile staminate portion of the spadix is noteworthy in being less than 2 mm long, with laxly arranged, fungiform, or deeply lobed flowers. The morphology of the style is not common in *Chlorospatha*, being appressed to the ovary and also long-attenuated.

Chlorospatha tokioensis would be most easily confused with *C. nicolsonii* from the Parque Nacional Natural Las Orquídeas on the western slopes of the Cordillera Occidental in Antioquia Department, Colombia, at 1500–1800 m elevation (see discussion under *C. nicolsonii*).

67. *Chlorospatha yatacuensis* Croat & L. P. Hannon, sp. nov. TYPE: Colombia. Valle: Yatacué, CVC camp at Anchicayá, 700–900 m, 3°40'N, 76°50'W, 25 Feb. 1983, A. Gentry, A. Juncosa & F. Gomez 40735 (holotype, MO-3031117!). Figure 48C.

Herba hemiepiphytica; cataphylla 8–23 cm longa. Petiolus ca. 63.5 cm longus, vaginatus per ca. 20 cm; lamina foliaris ovato-sagittata, ca. 34.5 × 19.5 cm; lobis posterioribus ca. 15 × 9 cm, nervis basalibus utroque 4, nervis primariis lateralibus utroque 4. Inflorescentiae 3 in quaque axilla, erecta; pedunculus 14.5–21 cm × 1.5–3 mm; spathe erecta, 4.2–5.5 cm longa, tubo 4–5 mm diam, lamina 2.2–3 cm × 4.5–6 mm; spadix 3.8–4.5 cm longus.

Hemiepiphytic herb; stem not known; internodes not known (all measurements made from dried material); cataphylls 8–23 cm long, obtuse with acumen at apex, drying weakly glossy to glossy, medium-dark to dark reddish brown. LEAVES 1; **petiole** 63.5 cm long, drying weakly glossy, blackish brown, the epidermis in part separated intact and semi-transparent, semiglossy, medium brown, sheathed ca. 20 cm, ca. 1/3 of total length; sheath decurrent at apex; free portion 5–7 mm diam. midway, terete; **blade** ovate-sagittate, ca. 34.5 × 19.5 cm, 1.8 times longer than wide, abruptly acuminate at apex, as broad at base as across

anterior lobe, drying thin, moderately bicolorous; upper surface drying matte, medium-dark olive-green; lower surface drying weakly glossy, pale-medium grayish green; anterior lobe 23 × 19.5 cm, 1.2 times longer than wide, 1.5 times longer than posterior lobes, broadest below middle, ± symmetrical; posterior lobes directed toward the base, ca. 15 × 9 cm, 1.6 times longer than wide, apex not known, broadest at base, moderately inequilateral, the inner side narrower, weakly rounded toward base, decurrent onto petiole, possibly weakly confluent with opposite lobe, with confluent portion obscuring petiole apex; outer side 1.6 to 2.7 times wider than inner side midway, ± straight toward base; midrib convex on lower surface, drying weakly raised, moderately darker than surface, darkest toward base; **basal veins** 4 pairs, coalesced into a prominent posterior rib; primary lateral veins 4 pairs, arising at 50°–65°, most acutely toward apex, moderately arcuate, drying ± flattened on lower surface, moderately darker than surface; secondary veins drying weakly raised on lower surface, weakly darker than surface; tertiary veins drying visible, distinct on lower surface, weakly darker than surface; reticulate veins drying obscure; collective veins 3 to 4, point of origin not known, ± parallel to and 3–7 mm from margin. INFLORESCENCES to 3 per axil, erect, possibly erect-spreading; sympodium possibly held within a sympodial cataphyll; sympodial cataphyll ca. 14 × ca. 2 cm, acuminate at apex, 1-ribbed abaxially; peduncle 14.5–21 cm × 1.5–3 mm, broadest toward base, drying weakly glossy to semiglossy, pale-medium brown, occasionally dark brown toward apex; **spathe** erect, cream-colored, 4.2–5.5 cm long, acuminate at apex, drying matte to weakly glossy, dark brown on both surfaces; spathe tube 2–2.5 cm × 4–5 mm; spathe blade 2.2–3 cm × 4.5–6 mm, marcescent, erect after anthesis; **spadix** erect, 3.8–4.5 cm long, sessile, adnate to spathe 8–10 mm at base, ca. 1/2 of the length of pistillate portion; pistillate portion 1.5–1.8 cm × 3–4 mm, broadest midway, drying medium reddish brown; fertile staminate portion 1.5–1.7 cm long, narrowly rounded at apex, weakly ellipsoid, drying medium-dark to dark reddish brown; sterile staminate portion 8–10 × 2.5–3 mm, ± cylindrical or weakly broadest at apex, drying dark blackish brown; pistils weakly coherent, ca. 3 to 4 across the axis (viewed from above), ca. 1.5–1.8 mm long; ovaries 1–1.3 × 1.5–1.8 mm, ± cylindrical or subglobose, obtusely truncate at apex, drying yellowish cream; style Type 9 (Fig. 1), 0.3–0.6 × 1.5–1.8 mm, broader than ovary apex, with most margins coherent with those of adjacent styles; **stigma** ca. 0.3 mm diam., weakly elevated on and

weakly broader than narrowed portion of style; synandria $1\text{--}1.3 \times 1.5\text{--}2$ mm, coherent, truncate, 3- to 4(5)-lobed, with narrowly sinuate margins, 3- to 4(5)-androus; sterile flowers ca. $1 \times 1\text{--}1.5$ mm, weakly elongated in direction of axis, coherent, truncate, \pm prismatic, in 7 to 8 whorls (a few flowers extending into pistillate portion). Berries not known.

Phenology. Flowering is only known to occur in *Chlorospatha yatacuensis* during the month of February.

Etymology. *Chlorospatha yatacuensis* is named for Yatacué, a town in the Parque Nacional de Farrallones in Valle Department of Colombia, near the area where the type of the new species was collected.

Discussion. *Chlorospatha yatacuensis* could possibly be one of the few species in which the sympodium is held within a sympodial cataphyll toward the base of the petiole. A prominent cataphyll appears to subtend the sympodium of this specimen, but since there is no morphological difference between sympodial or vegetative cataphylls, this condition cannot be confirmed, the sympodium having been removed from its associated leaf on the herbarium specimen. The petiole sheathing of 20 cm and peduncle lengths of 14.5–21 cm would easily accord with a plant whose peduncle is held within the sheath. It is hoped that additional collections will clarify the issue. The single herbarium specimen is further incomplete and also provides no information pertaining to the stem or its internodes.

Chlorospatha yatacuensis is known only from the type locality at the CVC camp at Anchicayá, near Yatacué in Valle Department, Colombia, in mature tropical wet forest or premontane wet forest on the western slopes of the Cordillera Occidental at 700–900 m elevation. The species would be expected to occur elsewhere within the department and to the north in Chocó and possibly southward into Cauca.

Chlorospatha yatacuensis, a member of *Chlorospatha* sect. *Occidentales*, is a moderately large plant, possibly 1 m tall, with the petiole 63.5 cm long and the leaf blade 34.5 cm long, drying an unusual pale-medium grayish green on the lower surface. The species is one of few hemiepiphytes in the genus and was collected on a stump. The species is distinguished by its broadly ovate-sagittate leaf blades with few primary lateral veins (four pairs), and broad, moderately long posterior lobes with the inner margins decurrent onto the petiole. The petiole is distinctive in drying with the epidermis partially separated intact from the main body and semi-transparent, and in being sheathed only one third of

its length. The peduncles are short, 14.5–21 cm long. Particularly noteworthy is the uncommonly small, entirely cream-colored inflorescence, 4.2–5.5 cm long, which would not be expected in such a large plant. Also unusual are the prismatic sterile flowers.

Chlorospatha yatacuensis could not be easily confused with any species, but could possibly be confused with *C. bayae*, which occurs in the same general area, but at higher elevations along the old Cali–Buenaventura road, 50.5 km north of Agua Clara, on the western slopes of the Cordillera Occidental in Valle Department, Colombia, at 1100–1200 m elevation (see discussion under *C. bayae*).

68. *Chlorospatha yaupiensis* Croat & L. P. Hannon, sp. nov. TYPE: Ecuador. Morona-Santiago: Cordillera de Cutucú, W slope, along Logroño–Yaupi trail, in the general region, 1600–1800 m, $2^{\circ}46'S$, $78^{\circ}06'W$, Nov. 1976, *M. Madison, M. Bush & W. Davis* 3359 (holotype, SEL-016544!). Figure 48D.

Herba ca. 50 cm; internodia 1.5–2.3 cm \times 8–10 mm; cataphylla usque ad 12 cm longa. Petiolus usque ad 36 cm longus, vaginatus per ca. 15 cm; lamina foliaris ovato-triangularis, subsagittata, ca. 21×14.5 cm, lobis posterioribus $8\text{--}8.5 \times$ ca. 5.5 cm, nervis basalibus utroque 2 vel 3, nervis primariis lateralibus utroque 3 vel 4. Inflorescentiae 4 in quaque axilla; pedunculus (12–)14.5–21 cm \times 1–2 mm; spathae tubo 2.4–3.2 cm \times 3.5–4 mm; spadix longitudine ignota.

Terrestrial herb, ca. 50 cm tall; stem decumbent, with remnants of old cataphylls persisting as pale linear fibers along its length (all measurements made from dried material); internodes 1.5–2.3 cm \times 8–10 mm, red, drying weakly glossy, medium brown; cataphylls to 12 cm long, apex not known, drying \pm fibrous. LEAVES 2 to 3; **petiole** to 36 cm long, reddish pink, granular-puberulent, crispy-puberulent toward apex, most densely so in apical 3 cm, drying matte, dark yellowish brown, sheathed ca. 15 cm, ca. 1/2 of total length; sheath decurrent at apex; free portion 3.5 mm diam. midway; **blade** ovate-triangular, subsagittate at base, 21×14.5 cm, 1.4 times longer than wide, bluntly acute at apex, broadest at base, ca. 1.5 times wider at base than across anterior lobe (measured tip to tip across posterior lobes), weakly constricted in area of petiole attachment, drying thinly coriaceous, weakly bicolorous; upper surface drying matte to weakly glossy, dark brown; lower surface reticulate, drying matte, with pale, linear cellular inclusions in developing blade; anterior lobe 16.5×11.8 cm, 1.4 times longer than wide, 1.9 to 2.1 times longer than posterior lobes, broadest at

base, \pm symmetrical; posterior lobes directed toward the base, $8\text{--}8.5 \times 5.5$ cm, 1.5 times longer than wide, broadly to narrowly rounded at apex, broadest at base, \pm symmetrical to weakly inequilateral, the inner side narrower, broadly rounded toward base, briefly attenuate onto posterior rib; outer side (1 to) 1.6 times wider than inner side midway, straight toward base; major and minor venation drying weakly prominulous on upper surface, entirely \pm crispy-puberulent to granular-puberulent on lower surface; midrib drying weakly convex in basal 3 cm on upper surface, prominently raised on lower surface, \pm crispy-puberulent, darker than surface; **basal veins** 2 to 3 pairs, coalesced into a prominent posterior rib; posterior rib naked 4–5 mm per side; primary lateral veins 3 to 4 pairs, arising at $30^\circ\text{--}50^\circ$, most acutely toward apex, weakly arcuate, drying prominently raised on lower surface, darker than surface; secondary and tertiary veins drying raised on lower surface, weakly darker than surface; reticulate veins drying prominulous on lower surface, weakly darker than surface; collective veins 3, the innermost arising from one of the lateral veins on inner side of posterior lobe, moderately scalloped, 4–9 mm from margin. **INFLORESCENCES** erect, to 4 per axil; peduncle held within the sheath, (12–)14.5–21 cm \times 1–2 mm, entirely crispy-puberulent, or in part only in apical 3–4 cm, and otherwise glabrous or granular-puberulent, drying matte, dark brown; **spathe** total length not known; spathe tube green, 2.4–3.2 cm \times 3.5–4 mm, weakly crispy-puberulent abaxially, drying matte, dark brown; spathe blade white; **spadix** total length not known, adnate to spathe 1.2–1.6 cm at base, ca. 1/2 of the length of pistillate portion; pistillate portion 2–3 cm \times 4–4.5 mm.; fertile staminate portion not known; sterile staminate portion not known; pistils weakly coherent, 3 across the axis (viewed from above), ca. 1 mm long; ovaries \pm cylindrical to obtusely obconical, 1.5 mm diam.; style Type 1 (Fig. 1), ca. 1.5 mm diam., as broad as ovary apex, the margins not coherent with those of adjacent styles; **stigma** sessile; synandria not known; sterile flowers not known. **INFRUCTESCENCE** 5.3 cm \times 9 mm; berries 3–4 mm diam.

Phenology. Flowering and fruiting are known to occur in *Chlorospatha yaupiensis* only during the month of November. The single collection has only an infructescence and two inflorescences past staminal anthesis, the staminate portion of the spadix and spathe blade having already abscised; therefore, little is known about the details of the flowers.

Etymology. The name refers to the Logroño–Yaupi trail in the Cordillera de Cutucú in Morona-

Santiago Province, Ecuador, where the type of *Chlorospatha yaupiensis* was collected.

Discussion. *Chlorospatha yaupiensis* is known only from the type locality in an area southeast of Logroño in Morona-Santiago Province, in lower montane wet forest on the western slopes of the Cordillera de Cutucú, east of the Andes, at 1600–1800 m elevation. The species would be expected to occur elsewhere in the Cutucú and perhaps nowhere else, the Cutucú being a region noted for a high level of endemism in species of Araceae.

Chlorospatha yaupiensis is a member of *Chlorospatha* sect. *Orientalis* and is distinguished by its ovate-triangular, subsagittate leaf blades that dry dark brown above, matte on both surfaces, and reticulate on the lower surface, with the posterior lobes broad, ca. 1.5 times longer than wide. All orders of venation dry more or less raised on the lower surface, crispy-puberulent to granular-puberulent, and darker than the surface. The indumentum also occurs on the peduncles, abaxial surface of the spathe tube, and apical portion of the petiole. The stem is red, a color not observed in any other species, and the petiole reddish pink, with the sheath comprising one half of its length. The peduncle is accordingly long, (12–)14.5–21 cm, unusual for species from the eastern slopes, most of which have peduncles less than 12 cm long.

Chlorospatha yaupiensis would be most easily confused with *C. cutucuensis*, with which it is sympatric in the area near Logroño, in the Cordillera de Cutucú (see discussion under *C. cutucuensis*).

CHLOROSPATHA SPECIES NOT FORMALLY PUBLISHED IN THIS REVISION

The following four species are distinct and validly new, but were collected in sterile condition and will be formally and completely described only after they have been collected again in fertile condition.

Chlorospatha sp. indet. 1. Colombia. Nariño: Mpio. Ricaurte, Altaquér–Tumaco rd., Río Ñambí, 7 km W of Altaquér, 1100–1130 m, $1^\circ 18'N$, $78^\circ 04'W$, 20 Mar. 1990, *Croat 71604* (MO).

Terrestrial herb, to ca. 40 cm tall (all measurements made from dried material); stem decumbent, erect 10 cm, with remnants of old cataphylls persisting \pm intact along its length; internodes $1\text{--}1.5 \times 1\text{--}1.5$ cm, semiglossy, dark green, drying weakly glossy, medium-dark brown; cataphylls not known. **LEAVES** 4, erect-spreading; **petioles** 18–25 cm long, moderately soft, glabrous, semiglossy, medium green, with weakly darker transverse

markings, drying weakly glossy, medium-dark brown, with epidermis in part separated \pm intact and semi-transparent, sheathed 8–10 cm, ca. 1/2 of total length; sheath decurrent at apex; free portion 4–6 mm diam. midway, terete, weakly and narrowly sulcate; **blades** broadly ovate, cordate at base, 15.5–18.5 \times 11.5–13 cm, 1.3 to 1.4 times longer than wide, apiculate at apex, broadest across anterior lobe, 1.6 to 1.7 times wider across anterior lobe than at base (measured tip to tip across posterior lobes), soft, thin, conspicuously bicolorous; upper surface quilted, velvety, dark green, drying matte to weakly glossy, medium-dark olive-green; lower surface matte, drying matte to weakly glossy, moderately paler; anterior lobe 10.5–13 \times 11.5–13 cm, as wide as long or weakly wider to weakly narrower than long (ca. 1 cm wider or narrower), 1.8 to 2.2 times longer than posterior lobes, broadest at or below middle, \pm symmetrical to weakly inequilateral, with one side to 8 mm wider than opposite side; posterior lobes directed toward the base, 5.8–6 \times 5.8–6 cm, about as wide as long, broadly rounded at apex, broadest at base, moderately to markedly inequilateral, the inner side narrower, weakly to broadly rounded toward base, briefly attenuate onto petiole apex, possibly weakly confluent with opposite lobe; outer side 2.3 to 4 times wider than inner side midway; midrib and major venation deeply sunken on upper surface, round-raised on lower surface, drying \pm flattened, moderately darker than surface; **basal veins** 3 to 4 pairs, coalesced into a prominent posterior rib; primary lateral veins 3(4) pairs, arising at 35°–55°, most acutely toward apex, moderately arcuate; secondary veins drying in part weakly raised to prominulous and otherwise flat on lower surface, \pm concolorous; tertiary veins flat on lower surface, distinct, darker than surface, drying \pm obscure; reticulate veins drying \pm obscure; collective veins 3, the innermost arising from one of the lowermost lateral veins on inner side of posterior lobe, loop-connected with all preceding lateral veins, \pm parallel to and 2.5–6 mm from margin. INFLORESCENCE erect; peduncle pale green; spathe tube matte, medium green toward base, semiglossy, dark purple at apex. Berries not known.

Phenology. Flowering is only known to occur in species indet. 1 during the month of March. The inflorescence was not examined.

Discussion. *Chlorospatha* sp. indet. 1 is known from a single, incomplete herbarium specimen, with label notes providing some details regarding the inflorescence. The collection was made in premontane wet forest on the western slopes of the Cordillera

Occidental in Nariño Department in southern Colombia, at 1100–1300 m elevation. It would be expected to occur southward into northern Ecuador.

Chlorospatha sp. indet. 1 is probably a member of *Chlorospatha* sect. *Occidentales* and is distinguished by its ovate-cordate, velvety, dark green leaf blades that are only slightly longer than wide, giving them a rounded appearance. It is also distinguished by its spathe tube, which is green toward the base and dark purple at the apex.

Chlorospatha sp. indet. 1 could possibly be confused with *C. besseae* in the sterile state, a species that occurs on the western slopes of the Andes in Carchi and Esmeraldas provinces in northern Ecuador (see discussion under *C. besseae*). The petiole of *C. besseae* is matte, entirely green, and moderately firm, differing from that of *Chlorospatha* sp. indet. 1, which is moderately soft, semiglossy, and green, with obscure, darker transverse markings. The petiole of the latter species dries weakly glossy, with the epidermis partially separated intact from the main body, whereas that of *C. besseae* dries matte, with no separation of the epidermis. The leaf blades are similar, but the blade of *C. besseae* is more elongated, with the inner margins of the posterior lobes decurrent onto the petiole. In *Chlorospatha* sp. indet. 1, the inner margin either terminates at the petiole apex or is possibly weakly confluent with that of the opposite lobe. The major venation on the lower surface of the blade of *Chlorospatha* sp. indet. 1 dries flattened, whereas that of *C. besseae* dries raised. The latter species has four to five(six) pairs of primary lateral veins versus three(four) pairs in *Chlorospatha* sp. indet. 1. The spathe tube of *C. besseae* is semiglossy, pale green to yellow-green, and that of *Chlorospatha* sp. indet. 1 is matte, medium green toward the base, and semiglossy, dark purple at the apex.

Additional specimen examined. COLOMBIA. **Nariño:** Mpio. Ricaurte, Altaquér–Tumaco rd., Río Ñambí, 7 km W of Altaquér, 1100–1130 m, 1°18'N, 78°04'W, 20 Mar. 1990, *Croat 71604* (MO).

***Chlorospatha* sp. indet. 2.** Colombia. Valle: along Queremal–Buenaventura rd., 28 km W of Queremal, 3 km W of Anchicayá, 220–230 m, 3°37'N, 76°58'W, 12 July 1997, *Croat & J. Gaskin 79751* (CUVC, MO).

Terrestrial herb, less than 1 m tall; stem not known; internodes short, to 2.7 cm diam. (all measurements made from dried material); cataphylls not known. LEAVES 2, erect-spreading; **petioles** ca. 40 cm long, glabrous, semiglossy, medium green, irregularly transversely lineate, less so toward apex, drying weakly glossy, dark brown, sheathed ca. 15

cm, slightly more than 1/3 of total length; sheath decurrent at apex, the sides erect; free portion 2–3.5 mm diam. midway, terete; **blades** sagittate, narrowly triangular, $29\text{--}31 \times 9.3\text{--}11.5$ cm, 2.7 to 3 times longer than wide, acuminate at apex, weakly broadest at base, 1.1 to 1.2 times broader at base than across anterior lobe (measured tip to tip across posterior lobes), weakly constricted in area of petiole attachment (at least on one side), subcoriaceous, prominently bicolorous; upper surface glossy, dark green, drying weakly glossy, medium-dark yellow-brown; lower surface weakly glossy, drying matte, brownish cream, prominently paler; anterior lobe $19.5\text{--}21 \times 9.3\text{--}10$ cm, 2.1 times longer than wide, 1.8 to 1.9 times longer than posterior lobes, broadest below middle, \pm symmetrical; posterior lobes directed toward the base, $10.5\text{--}12 \times 4\text{--}4.6$ cm, 2.5 to 2.8 times longer than wide, acute to bluntly acute at apex, broadest at base, weakly to moderately inequilateral, the inner side narrower, weakly rounded toward base, narrowly attenuate and decurrent onto petiole; outer side 1.2 to 2.1 times wider than inner side midway; midrib deeply sunken on upper surface, round-raised on lower surface, drying raised, moderately darker than surface; **basal veins** 4 pairs, coalesced into prominent posterior rib; primary lateral veins 4 pairs, arising at $30^\circ\text{--}65^\circ$, most acutely toward apex, weakly to moderately arcuate, etched on upper surface, convex on lower surface, drying weakly raised and \pm flattened, moderately darker than surface; secondary veins drying in part weakly raised on lower surface, otherwise flat or weakly prominulous, concolorous to weakly darker than surface; tertiary veins visible, distinct on lower surface, moderately darker than surface, drying flat, visible, concolorous to weakly darker than surface; reticulate veins drying flat, in part visible on lower surface, \pm concolorous; collective veins 3 to 4, the innermost arising from the lowermost lateral vein on inner side of posterior lobe, loop-connected with all preceding lateral veins, \pm parallel to and 3–7 mm from margin. INFLORESCENCE not known. Berries not known.

Chlorospatha sp. indet. 2 is known from a single sterile collection made near Anchicayá in Valle Department, Colombia, in either tropical wet forest or premontane wet forest on the western slopes of the Andes at 220–230 m elevation. The species is probably a member of *Chlorospatha* sect. *Occidentales* and is distinguished by its narrowly triangular-sagittate leaf blades that are conspicuously bicolorous in both living and dried material, with the lower surface drying matte and markedly pale brownish cream.

Chlorospatha sp. indet. 2 would be most easily confused with *Chlorospatha* sp. indet. 4 and *C.*

nicolsonii, all three species having long, narrow posterior lobes. However, the blades of the latter two species dry concolorous to only moderately bicolorous, with the lower surface weakly glossy to semiglossy. The blades of *Chlorospatha* sp. indet. 2 have four pairs of primary lateral veins and dry yellow-brown, whereas those of *Chlorospatha* sp. indet. 4 have two or three pairs and dry yellow-green. The blades of *C. nicolsonii* are subhastate, with the posterior lobes directed outward, not toward the base as they are in *Chlorospatha* sp. indet. 2, and much narrower, 3.4 to 3.8 times longer than wide versus 2.5 to 2.8 times longer than wide in *Chlorospatha* sp. indet. 2, which has narrowly triangular blades.

Additional specimen examined. COLOMBIA. Valle: along Queremal–Buenaventura rd., 28 km W of Queremal, 3 km W of Anchicayá, 220–230 m, $3^\circ 37'N$, $76^\circ 58'W$, 12 July 1997, Croat & J. Gaskin 79751 (CUVC, MO).

Chlorospatha sp. indet. 3. Colombia. Valle: along Queremal–Anchicayá rd., 3 km W of Queremal, 1400 m, $3^\circ 31'N$, $76^\circ 44'W$, 10 July 1997, Croat & J. Gaskin 79662 (CUVC, MO).

Terrestrial herb, ca. 50 cm tall; stem with internodes ca. 1×1.5 cm (all measurements made from dried material); cataphylls ultimately deciduous. LEAVES 1 (probably erect-spreading); **petiole** 32 cm long, spongy, glabrous, pale green, drying weakly glossy, dark brown, sheathed ca. 22 cm, ca. 2/3 of total length; sheath decurrent at apex; free portion 3–5 mm diam. midway, terete; **blade** sagittate-subhastate, 20.5×13.5 cm, 1.5 times longer than wide, briefly acuminate at apex, broadest at base, 1.4 times wider at base than across anterior lobe (measured tip to tip across posterior lobes), thinly coriaceous, drying \pm concolorous; upper surface semiglossy, green, drying weakly glossy, dark yellowish brown; lower surface glossy, drying semiglossy to glossy; anterior lobe 14.5×9.5 cm, 1.5 times longer than wide, 1.7 times longer than posterior lobes, broadest below middle, \pm symmetrical; posterior lobes directed somewhat outward, 8.5×4.5 cm, 1.9 times longer than wide, bluntly acute at apex, broadest at base, moderately inequilateral, the inner side narrower, weakly rounded toward base, briefly attenuate onto posterior rib; outer side ca. 2 times wider than inner side midway, weakly concave toward base; midrib sunken on upper surface, round-raised on lower surface, paler than surface, drying weakly raised and \pm flattened, weakly darker than surface; **basal veins** 4 pairs, coalesced into a prominent posterior rib; posterior rib naked ca. 6 mm per side; primary lateral veins 7 to 8 pairs, arising at $55^\circ\text{--}65^\circ$, weakly to moderately arcuate, etched on upper

surface, convex on lower surface, drying \pm flattened, weakly darker than surface; secondary veins drying weakly prominulous on lower surface, \pm concolorous; tertiary veins drying in part weakly prominulous on lower surface, otherwise flat, \pm concolorous; reticulate veins drying obscure; collective veins 3, the innermost arising from one of the lowermost lateral veins on inner side of posterior lobe, loop-connected with all preceding lateral veins, \pm parallel to and 3–6 mm from margin. INFLORESCENCES 2 per axil; spathe tube green on outer surface; spathe blade white on outer surface. Berries not known.

Phenology. Flowering is only known to occur in *Chlorospatha* sp. indet. 3 during the month of July. The inflorescence was not examined.

Discussion. *Chlorospatha* sp. indet. 3 is known from a single collection made in premontane wet forest on the western slopes of the Cordillera Occidental, near Queremal in Valle Department, Colombia, at 1400 m elevation. The specimen examined was sterile, with label notes indicating the color of the spathe. The species is probably a member of *Chlorospatha* sect. *Occidentales* and is distinguished by its sagittate-subhastate leaf blades that are flat (not quilted) on the upper surface, with the midrib and major veins etched, and dry weakly glossy, yellowish brown, with the lower surface somewhat glossy and all orders of venation somewhat flattened. The posterior lobes are moderately broad, less than two times longer than wide, and bluntly acute at the apex. The petiole is noteworthy in being sheathed two thirds of its length, although the specimen is sterile.

Chlorospatha sp. indet. 3 could possibly be confused with *C. bayae*, also from Valle, and *C. jaramilloi* from Pichincha Province, Ecuador. All three species have moderately broad posterior lobes, but those of *C. bayae* and *C. jaramilloi* are directed more toward the base, less tapered and more rounded at the apex. The blades of the latter two species dry green or greenish, with the abaxial venation more or less raised, whereas those of *Chlorospatha* sp. indet. 3 dry yellowish brown, with most abaxial venation flattened. The spathe tube of *Chlorospatha* sp. indet. 3 is green, differing from those of *C. bayae* and *C. jaramilloi*, which are entirely or mostly purple.

Additional specimen examined. COLOMBIA. **Valle:** along Queremal–Anchicayá rd., 3 km W of Queremal, 1400 m, 3°31'N, 76°44'W, 10 July 1997, *Croat & J. Gaskin* 79662 (CUVC, MO).

***Chlorospatha* sp. indet. 4.** Colombia. Chocó: Cerro del Torrá, E bank of Río Negro, below Heliport,

1000–1900 m, 22 Aug. 1988, *J. Ramos et al.* 1470 (CUVC, MO); along Bolívar–Quibdó rd., 23 mi. W of Bolívar, on S bank of Río Atrato, 1600 m, 5°50'N, 76°15'W, 16 Dec. 1980, *Croat & A. Cogollo* 52047 (MO).

Terrestrial herb, to 70 cm tall; stem decumbent, ca. 25 cm long, with some remnants of old cataphylls persisting semi-intact along its length (all measurements made from dried material); internodes 1.2–4 cm \times 5–10 mm, drying matte to weakly glossy, medium grayish tan to dark reddish brown; cataphylls 6.5–10 cm long, cuspidate at apex, drying weakly glossy to semiglossy, dark reddish brown. LEAVES 1 to 3, erect-spreading; **petioles** 23–25(–43) cm long, glabrous, greenish purple, drying matte to weakly glossy, dark reddish brown, sheathed 8–10.5 cm, ca. 1/3 to 1/2 of total length; sheath decurrent at apex; free portion 2–3 mm diam. midway, terete; **blades** sagittate, 24.5–30 \times 9–10.8 cm, 2.7 to 2.8 times longer than wide, acuminate or apiculate at apex, as broad as or weakly narrower at base than across anterior lobe (measured tip to tip across posterior lobes), weakly or not at all constricted in area of petiole attachment, drying thinly coriaceous, \pm concolorous to weakly bicolorous; upper surface drying weakly glossy, medium-dark brownish yellow-green; lower surface drying semiglossy; anterior lobe 15–16.5(–20) \times 9–10.8 cm, 1.5 to 1.7 times longer than wide, 1.2 to 1.4 times longer than posterior lobes, broadest at or below middle, weakly inequilateral; posterior lobes directed prominently toward the base, 10.5–13.5(–16) \times 4–4.8 cm, 2.4 to 2.8 times longer than wide, bluntly acute to narrowly rounded at apex, broadest at base, weakly to moderately inequilateral, the inner side narrower, \pm acute toward base, briefly attenuate and weakly confluent with opposite lobe, the confluent portion obscuring the petiole apex; outer side 1.2 to 1.9 times wider than inner side midway, \pm straight toward base; midrib round-raised on lower surface, drying raised, weakly to moderately darker than surface; **basal veins** 6 to 7 pairs, coalesced into a prominent posterior rib; primary lateral veins 2 to 3(4) pairs, arising at 35°–50°, weakly to prominently arcuate, convex on lower surface, drying weakly raised to \pm flattened, weakly to moderately darker than surface; secondary veins raised on lower surface, drying weakly raised, weakly darker than surface; tertiary veins drying weakly prominulous on lower surface, concolorous to weakly darker than surface; reticulate veins drying obscure; collective veins 3, the innermost arising from one of the lowermost lateral veins on inner side of posterior lobe, loop-connected with all preceding lateral veins, \pm parallel to and 3–7

mm from margin. INFLORESCENCE (not examined) 1 per axil; peduncle 9 cm long; spathe 15 cm long. Berries not known.

The specimen examined, *J. Ramos et al. 1470* (MO), was sterile; however, the label notes report that the collection was in flower during the month of August.

Chlorospatha sp. indet. 4 is known from two localities in lower montane rainforest and lower montane wet forest on the western slopes of the Cordillera Occidental in Chocó Department, Colombia, at 1000–1900 m elevation. *J. Ramos et al. 1470* is from the Cerro del Torrá, along the banks of the Río Negro. *Croat & A. Cogollo 52047* is from farther north, approximately 23 miles west of Bolívar, along the banks of the Río Atrato. The species would be expected to occur elsewhere within the department, possibly along watercourses.

Chlorospatha sp. indet. 4 is probably a member of *Chlorospatha* sect. *Occidentales* and is distinguished by its brownish yellow-green-drying, narrowly sagittate leaf blades that are usually narrower at the base than across the anterior lobe, with the posterior lobes directed prominently toward the base. The posterior lobes are long and moderately narrow, with the anterior lobe only slightly longer, and the inner margins weakly confluent across the petiole apex at the base. The species is unusual in having few primary lateral veins, relative to blade size, only two or three pairs, which are frequently prominently arcuate, rarely with a fourth vein on one side. The most distinguishing feature is possibly the unusual combination of a short peduncle (9 cm long) and remarkably long spathe, 15 cm long. However, this could not be confirmed, the information having come from the label notes. Such a combination would be unique in *Chlorospatha*. It could be argued that this combination of characters would not be unusual in *Xanthosoma*, but the other characters appear to better accord with *Chlorospatha*. *Chlorospatha* sp. indet. 4 is a small plant, less than 1 m tall, with long, narrow internodes and the remnants of old cataphylls persisting semi-intact along the length of the stem. These characters are more typical of *Chlorospatha*.

Chlorospatha sp. indet. 4 is most similar to *C. nicolsonii* from the Parque Nacional Natural Las Orquídeas in Antioquia Department to the north, at 1500–1800 m elevation on the western slopes of the Cordillera Occidental. Both species have long internodes, short peduncles, and relatively few pairs of primary lateral veins, two or three in *Chlorospatha* sp. indet. 4 versus three or four in *C. nicolsonii*. The leaf blades of *C. nicolsonii* are subhastate and dry brown, with narrower posterior lobes (3.4 to 3.8 times

longer than wide) with the inner margins decurrent onto the petiole. Species 4 differs in having leaf blades that dry yellow-green, with the posterior lobes directed prominently toward the base, broader (2.4 to 2.8 times longer than wide) and the inner margins weakly confluent across the petiole apex. The inflorescence of *C. nicolsonii* is significantly smaller, 7–8.5 cm long versus 15 cm long in *Chlorospatha* sp. indet. 4.

Additional specimen examined. COLOMBIA. **Chocó:** Cerro del Torrá, E bank of Río Negro, below Heliport, 1000–1900 m, 22 Aug. 1988, *J. Ramos et al. 1470* (CUVC, MO); along Bolívar–Quibdó rd., 23 mi. W of Bolívar, on S bank of Río Atrato, 1600 m, 5°50'N, 76°15'W, 16 Dec. 1980, *Croat & A. Cogollo 52047* (MO).

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Appendix 1. List of species, subspecies, and varieties accepted for the genus *Chlorospatha* Engl.

1. *Chlorospatha amalfiensis* Croat & L. P. Hannon
2. *Chlorospatha antioquiensis* Croat & L. P. Hannon
3. *Chlorospatha atropurpurea* (Madison) Madison
4. *Chlorospatha bayae* Croat & L. P. Hannon
5. *Chlorospatha besseae* Madison
6. *Chlorospatha betancurii* Croat & L. P. Hannon
7. *Chlorospatha bogneri* Croat & L. P. Hannon
8. *Chlorospatha boosii* Croat & L. P. Hannon
9. *Chlorospatha bullata* Croat & L. P. Hannon
10. *Chlorospatha caldasensis* Croat & L. P. Hannon
11. *Chlorospatha caliensis* Croat & L. P. Hannon

12. *Chlorospatha callejasii* Croat & L. P. Hannon
13. *Chlorospatha carchiensis* Croat & L. P. Hannon
14. *Chlorospatha castula* (Madison) Madison
15. *Chlorospatha cedralensis* Croat & L. P. Hannon
16. *Chlorospatha chocoensis* Croat & L. P. Hannon
17. *Chlorospatha cogolloi* Croat & L. P. Hannon
18. *Chlorospatha congensis* Croat & L. P. Hannon
19. *Chlorospatha corrugata* Bogner & Madison
20. *Chlorospatha croatiana* Grayum
20a. *Chlorospatha croatiana* Grayum subsp. *croatiana*
20b. *Chlorospatha croatiana* var. *enneaphylla* Grayum
21. *Chlorospatha cutucuensis* Madison
22. *Chlorospatha dodsonii* (G. S. Bunting) Madison
23. *Chlorospatha engleri* Croat & L. P. Hannon
24. *Chlorospatha feuersteiniae* (Croat & Bogner) Bogner & L. P. Hannon
25. *Chlorospatha gentryi* Grayum
26. *Chlorospatha giraldoi* Croat & L. P. Hannon
27. *Chlorospatha grayumii* Croat & L. P. Hannon
28. *Chlorospatha hammeliana* Grayum & Croat
29. *Chlorospatha hannoniae* Croat
30. *Chlorospatha hastata* Croat & L. P. Hannon
31. *Chlorospatha hastifolia* Bogner & L. P. Hannon
32. *Chlorospatha huilensis* Croat & L. P. Hannon
33. *Chlorospatha ilensis* Madison
34. *Chlorospatha jaramilloi* Croat & L. P. Hannon
35. *Chlorospatha kolbii* Engl.
36. *Chlorospatha kressii* Grayum
37. *Chlorospatha lehmannii* (Engl.) Madison
38. *Chlorospatha limonensis* Croat & L. P. Hannon
39. *Chlorospatha litensis* Croat & L. P. Hannon
40. *Chlorospatha longiloba* Croat & L. P. Hannon
41. *Chlorospatha longipoda* (K. Krause) Madison
42. *Chlorospatha luteynii* Croat & L. P. Hannon
43. *Chlorospatha macphersonii* Croat & L. P. Hannon
44. *Chlorospatha maculata* Croat & L. P. Hannon
45. *Chlorospatha mansellii* Croat & L. P. Hannon
46. *Chlorospatha mirabilis* (Mast.) Madison
47. *Chlorospatha morae* Croat & L. P. Hannon
48. *Chlorospatha munchiquensis* Croat & L. P. Hannon
49. *Chlorospatha nambiensis* Croat & L. P. Hannon
50. *Chlorospatha narinoensis* Croat & L. P. Hannon
51. *Chlorospatha nicolsonii* Croat & L. P. Hannon
52. *Chlorospatha noramurphyae* Croat & L. P. Hannon
53. *Chlorospatha oblongifolia* Croat & L. P. Hannon
54. *Chlorospatha planadensis* Croat & L. P. Hannon
55. *Chlorospatha plowmanii* (Madison) Croat & L. P. Hannon
56. *Chlorospatha portillae* Croat & L. P. Hannon
57. *Chlorospatha pubescens* Croat & L. P. Hannon
58. *Chlorospatha queremalensis* Croat & L. P. Hannon
59. *Chlorospatha ricaurtensis* Croat & L. P. Hannon
60. *Chlorospatha risaraldensis* Croat & L. P. Hannon
61. *Chlorospatha sagittata* Croat & L. P. Hannon
62. *Chlorospatha sizemoreae* Croat & L. P. Hannon
63. *Chlorospatha stellararreae* Croat & L. P. Hannon

64. *Chlorospatha sucumbensis* Croat & L. P. Hannon
65. *Chlorospatha timbiquensis* Croat & L. P. Hannon
66. *Chlorospatha tokioensis* Croat & L. P. Hannon
67. *Chlorospatha yatacuensis* Croat & L. P. Hannon
68. *Chlorospatha yaupiensis* Croat & L. P. Hannon

Appendix 2. Index to exsiccatae. The numbers in parentheses refer to the numbered taxon in Appendix 1. Type specimens are indicated in boldface.

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Vargas 5363 (25).

Yanez & Shuigra 846 (53).

Zak 1601 (22).

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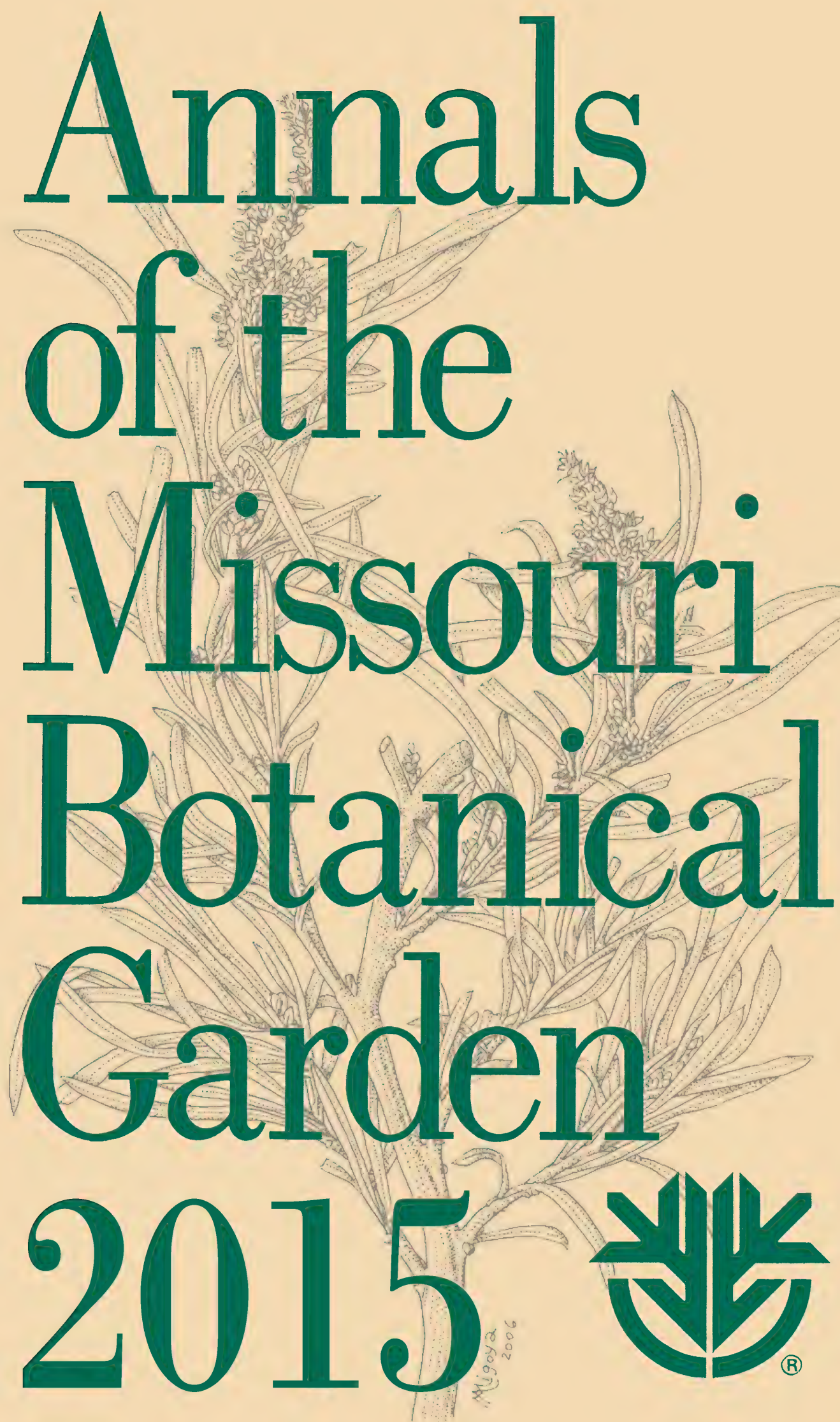
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REVISIÓN TAXONÓMICA DE LAS ESPECIES MONOICAS DE
AMARANTHUS
(AMARANTHACEAE):
AMARANTHUS SUBG.
AMARANTHUS Y *AMARANTHUS*
SUBG. *ALBERSIA*¹

RESUMEN

El género *Amaranthus* L. (Amaranthaceae) se caracteriza por presentar hierbas monoicas o dioicas, con hojas alternas, flores unisexuales protegidas por brácteas y bractéolas, generalmente tres a cinco sépalos glabros, estambres libres y fruto un utrículo o pixidio. En el presente tratamiento se realiza la revisión taxonómica de las especies monoicas del género *Amaranthus*, esto es las que conforman *Amaranthus* subg. *Amaranthus* (13 especies) y *Amaranthus* subg. *Albersia* (Kunth) Gren. & Godr. (52 especies). Cuarenta y seis de estas 65 especies son americanas, mientras que las restantes (19) son de África, Australia o Eurasia. Se establecen las siguientes nuevas sinonimias: *A. artineanus* Muschl. se considera sinónimo de *A. hybridus* L. subsp. *quitensis* (Kunth) Costea & Carretero y *A. chihuahuensis* S. Watson sinónimo de *A. torreyi* (A. Gray) S. Watson. Se proponen nombres en nuevos rangos (elevados de variedades a subespecies) para: *A. asplundii* Thell. subsp. *australis* (Hunz.) N. Bayón, *A. blitum* L. subsp. *pseudogracilis* (Thell.) N. Bayón, *A. crassipes* Schltdl. subsp. *warnockii* (I. M. Johnst.) N. Bayón y *A. macrocarpus* Benth. subsp. *pallidus* (Benth.) N. Bayón. Se designan lectotipos (15) para *Amarantellus argentinus* Speg., *Amaranthus albomarginatus* Uline & W. L. Bray, *A. asplundii* Thell., *A. ataco* Thell., *A. bigelovii* Uline & W. L. Bray, *A. blitum* L. subsp. *emarginatus* (Uline & W. L. Bray) Carretero, Muñoz Garmendia & Pedrol, *A. bracteosus* Uline & W. L. Bray, *A. caudatus* L. var. *alopecurus* Moq., *A. graecizans* L. subsp. *aschersonianus* (Thell.) Costea, D. M. Brenner & Tardif, *A. schinzianus* Thell., *A. sclerantoides* (Andersson) Andersson, *A. squamulatus* (Andersson) B. L. Rob., *A. wrightii* S. Watson, *Amblogyna squarrulosa* A. Gray y *Sarratia* Moq. Se designa neotipo para *A. vulgarissimus* Speg. y epitipo para *A. ascendens* Loisel. Se ilustran por primera vez en forma completa a 14 especies, y a otras ocho de las que sólo existían ilustraciones parciales.

ABSTRACT

The genus *Amaranthus* L. (Amaranthaceae) is characterized by its monoecious or dioecious herbs, with alternate leaves, unisexual flowers protected by bracts and bracteoles, usually three to five glabrous sepals, free stamens, and fruit a utricle or

¹ Este trabajo de revisión fue posible gracias a la colaboración de los curadores de herbario que facilitaron en préstamo especímenes, enviaron imágenes y brindaron su asesoramiento. Deseo reconocer los comentarios esclarecedores de Daniel Giuliano (LPAG) sobre cuestiones vinculadas con la nomenclatura y la tipificación durante la corrección final del manuscrito. Mi agradecimiento a los revisores, Katherine Waselkov, Jon Ricketson y un tercer revisor anónimo, como así también a la editora, Victoria Hollowell, por los valiosos comentarios que permitieron corregir y mejorar el manuscrito. Finalmente, deseo expresar un agradecimiento especial a Susana Freire por su guía y apoyo permanente durante la ejecución del trabajo y a Alejandra Migoya por su invaluable colaboración con las ilustraciones.

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pyxidium. A taxonomic revision of the monoecious species of *Amaranthus* is presented for those species that comprise *Amaranthus* subg. *Amaranthus* (13 species) and *Amaranthus* subg. *Albersia* (Kunth) Gren. & Godr. (52 species). Forty-six of these 65 species are American, while the rest (19) are from Africa, Australia, and Eurasia. The following taxa are newly synonymized: *A. artineanus* Muschl. with *A. hybridus* L. subsp. *quitensis* (Kunth) Costea & Carretero and *A. chihuahuensis* S. Watson with *A. torreyi* (A. Gray) S. Watson. Names at new rank (varieties elevated to subspecies) are proposed for *A. asplundii* Thell. subsp. *australis* (Hunz.) N. Bayón, *A. blitum* L. subsp. *pseudogracilis* (Thell.) N. Bayón, *A. crassipes* Schldl. subsp. *warnockii* (I. M. Johnst.) N. Bayón, and *A. macrocarpus* Benth. subsp. *pallidus* (Benth.) N. Bayón. Fifteen lectotypes are newly designated for *Amarantellus argentinus* Speg., *Amaranthus albomarginatus* Uline & W. L. Bray, *A. asplundii* Thell., *A. ataco* Thell., *A. bigelovii* Uline & W. L. Bray, *A. blitum* L. subsp. *emarginatus* (Uline & W. L. Bray) Carretero, Muñoz Garmendia & Pedrol, *A. bracteosus* Uline & W. L. Bray, *A. caudatus* L. var. *alopecurus* Moq., *A. graecizans* L. subsp. *aschersonianus* (Thell.) Costea, D. M. Brenner & Tardif, *A. schinzianus* Thell., *A. sclerantoides* (Andersson) Andersson, *A. squamulatus* (Andersson) B. L. Rob., *A. wrightii* S. Watson, *Amblogyna squarrulosa* A. Gray, and *Sarratia* Moq. A neotype is designated for *A. vulgatissimus* Speg. and an epitype is designated for *A. ascendens* Loisel. Complete illustrations are offered for 14 species never illustrated before, and for another eight species that were only partially illustrated in the past.

Key words: *Amaranthaceae*, *Amaranthus*, *Amaranthus* subg. *Albersia*.

El género *Amaranthus* L. (Amaranthaceae) comprende 75 especies ampliamente distribuidas en las regiones tropicales y templadas de todos los continentes, con una mayor concentración de especies en América. Son plantas C₄ de hábito herbáceo, monoicas o dioicas, con flores de perianto simple, calicoide, reunidas en inflorescencias variables, cuyas unidades elementales están constituidas por dicasios. *Amaranthus* se diferencia de los géneros más afines, *Chamissoa* Kunth y *Herbstia* Sohmer, por presentar flores imperfectas y estambres libres hasta la base. Según Mosyakin y Robertson (1996, 2003) se compone de tres subgéneros: *Amaranthus* subg. *Amaranthus* L., *Amaranthus* subg. *Acnida* (L.) Aellen ex K. R. Robertson y *Amaranthus* subg. *Albersia* (Kunth) Gren. & Godr.

Las especies monoicas tratadas en el presente estudio se corresponden con *Amaranthus* subg. *Amaranthus* y *Amaranthus* subg. *Albersia*. *Amaranthus* subg. *Amaranthus* comprende 13 especies de plantas erectas con inflorescencias terminales, flores pistiladas con cinco sépalos y frutos dehiscentes. Por su parte, *Amaranthus* subg. *Albersia* incluye 52 especies de plantas regularmente postradas con inflorescencias axilares, flores pistiladas con uno a cinco sépalos y frutos por lo general indehiscentes. El tercer subgénero, *Amaranthus* subg. *Acnida*, comprende un conjunto de 10 especies dioicas estudiadas detalladamente por Sauer (1955) y que no han sido incluidas en el presente trabajo.

Para las especies monoicas sólo existen hasta el momento estudios parciales. Entre ellos se destacan los de Sauer (1950, 1967), quien trató principalmente a las especies empleadas como pseudocereales. Hunziker (1951a, 1965, 1966) publicó trabajos referidos a las especies americanas, Aellen (1959) efectuó el tratamiento florístico del género para Europa, mientras Brenan (1961, 1981) hizo lo propio para Gran Bretaña y Sudáfrica. Uline y Bray (1894a,

1894b), Standley (1917) y Mosyakin y Robertson (2003) estudiaron al género para la flora de América del Norte y Thellung (1919a) para la flora europea. Costea et al. (2001a) realizaron una revisión preliminar de seis especies del complejo de *A. hybridus* L. Recientemente, Palmer (2009) se abocó al tratamiento de las especies de Australia. Debido a que el estudio completo de las especies monoicas no ha sido efectuado hasta el presente, se justifica la realización del mismo, el que sumado al aporte brindado por Sauer (1955) otorgaría un conocimiento íntegro del género *Amaranthus*.

HISTORIA TAXONÓMICA

El género *Amaranthus* fue establecido en 1753 por Linneo. Kunth (1838) crea el género *Albersia* Kunth para ubicar a las especies de *Amaranthus* s.l. que poseen frutos indehiscentes en el que reubica a *A. blitum* L. Uno de los autores que estudió más exhaustivamente al género fue Moquin (1849), quien lo ubicó en la tribu Achyrantheae Fenzl in Endl. y lo dividió en dos secciones: *Amaranthus* secc. *Euamaranthus* y *Amaranthus* secc. *Pyxidium* Moq. Asimismo, incluyó en su tratamiento a los géneros *Acnida* L., *Amblogyna* Raf., *Euxolus* Raf., *Sarratia* Moq., *Mengea* Schauer y *Scleropus* Schrad., cuyas especies se incluyen hoy dentro del género *Amaranthus*. Grenier y Godron (1855) consideran al género *Albersia* como un subgénero de *Amaranthus* (*Amaranthus* subg. *Albersia* (Kunth) Gren. & Godr.).

Urban (1924) crea el género *Goerziella* Urb., al que transfiere una sola especie: *Amaranthus minimus* Standl. Posteriormente, Sauer (1950, 1967) trata la historia, la taxonomía y la distribución geográfica de los amarantos empleados como pseudocereales y de las especies emparentadas. Hunziker (1951a) describe cuatro nuevas especies (*A. cardenasianus* Hunz., *A. kloosianus* Hunz., *A.*

lombardoi Hunz. y *A. persimilis* Hunz.). En 1965 efectúa la revisión parcial de nueve especies americanas con inflorescencias axilares. Posteriormente, en 1966, describe una nueva especie: *A. rosengurttii* Hunz. En ninguno de los tres trabajos mencionados, el autor especifica la posición infragenérica de las especies. Aellen (1959) incluye dentro de *Amaranthus* subg. *Amaranthus* a todas las especies monoicas y dentro de *Amaranthus* subg. *Acnida* a las especies dioicas.

Robertson (1981) apoya a Aellen (1959) en el sentido de que las especies del género *Amaranthus* que son monoicas deberían incluirse en el subgénero *Amaranthus*, mientras que las que son dioicas deberían serlo en el subgénero *Acnida*, en *Amaranthus*. Basándose en el carácter de dioecia y la distribución geográfica (circunscrita a América del Norte) apoya la idea de la existencia de este último subgénero. Además, considera que dentro del subgénero *Amaranthus* existen dos secciones: *Amaranthus* secc. *Amaranthus* L., con inflorescencias terminales grandes y frutos dehiscentes, y *Amaranthus* secc. *Blitopsis* Dumort., con inflorescencias mayoritariamente en glomérulos axilares y frutos indehiscentes.

Carretero (1985) justifica la creación de *Amaranthus* secc. *Pyxidium* Moq., con flores agrupadas en glomérulos axilares pero con frutos dehiscentes. De esta forma, para él, el subgénero *Amaranthus* queda constituido por tres secciones: *Amaranthus* secc. *Amaranthus*, *Amaranthus* secc. *Blitopsis* y *Amaranthus* secc. *Pyxidium*. Eliasson (1988) estima correcta la inclusión de los amarantos dioicos dentro del género *Amaranthus*, al mismo tiempo que comparte su segregación en un subgénero aparte: *Amaranthus* subg. *Acnida*. Por otra parte, juzga como no natural a la división de los amarantos monoicos en dos secciones.

Mosyakin y Robertson (1996) identifican la existencia de tres subgéneros dentro de *Amaranthus* (*Amaranthus* subg. *Amaranthus*, *Amaranthus* subg. *Acnida* y *Amaranthus* subg. *Albersia*) y reconocen secciones dentro de cada uno de ellos. Además, le dan a *Goerziella* rango de sección (monotípica), la que pasa a integrar *Amaranthus* subg. *Albersia*. Estos dos autores crean también *Amaranthus* nothosecc. *Dubia* Mosyakin & K. R. Robertson (monotípica) en la que incluyen a la especie de origen aloploiploide *A. dubius* Mart. ex Thell., dentro de *Amaranthus* subg. *Amaranthus*. Finalmente, reconocen que en todo el género, la dehiscencia o indehiscencia de los frutos es un carácter un tanto variable y no del todo seguro desde el punto de vista taxonómico.

Costea et al. (2001a) reconocen la existencia de tres subgéneros dentro de *Amaranthus*: *Amaranthus* subg. *Amaranthus*, *Amaranthus* subg. *Albersia* (ambos con especies monoicas) y *Amaranthus* subg. *Acnida* (con especies dioicas). Mosyakin y Robertson (2003) al tratar al género en la Flora de América del Norte, apoyan la existencia de dos subgéneros para las especies monoicas: *Amaranthus* subg. *Albersia* y *Amaranthus* subg. *Amaranthus*. En la Tabla 1 se presentan en forma comparativa las diferentes propuestas clasificatorias para el género *Amaranthus*.

UBICACIÓN SISTEMÁTICA DEL GÉNERO *AMARANTHUS*

El género *Amaranthus* se ubica en la familia Amaranthaceae Juss. y dentro de la subfamilia Amaranthoideae Burnett por el hecho de presentar anteras tetra-esporangiadas, biloculares al momento de la anthesis, mostrando dos líneas de dehiscencia. Por el contrario, la subfamilia Gomphrenoideae Kostel. posee anteras biesporangiadas, uniloculares al momento de la anthesis, mostrando una única línea de dehiscencia. Esta clasificación fue propuesta por Schinz (1893) y reafirmada por Covas (1939), Robertson (1981), Eliasson (1988) y Townsend (1993). Dentro de las Amaranthoideae, el género *Amaranthus* se ubica en la tribu Amarantheae Rchb. (Schinz, 1893) la que se caracteriza por poseer ovario uniovulado (siendo multiovulado en la tribu Celosieae Fenzl in Endl.) y en la subtribu Amaranthinae Fenzl in Endl., con semillas erectas, esto es con la radícula dirigida hacia abajo, y hojas alternas. Las semillas invertidas con radícula dirigida hacia arriba y con hojas comúnmente opuestas son características de la subtribu Aervinae Fenzl in Endl. (= Achyranthinae Benth. & Hook. f.).

RELACIONES GENÉRICAS

La subtribu Amaranthinae Fenzl. se caracteriza por sus semillas erectas, con la radícula dirigida hacia abajo y hojas alternas. Los principales caracteres que permiten distinguir al género *Amaranthus* entre los restantes que componen la subtribu son: por un lado *Amaranthus* posee flores imperfectas (sólo *Charpentiera* posee flores funcionalmente imperfectas), mientras que los géneros restantes las poseen perfectas. Por otro lado, *Amaranthus* presenta los estambres libres desde la base, no unidos para formar una copa o tubo, mientras que los otros géneros los tienen soldados al menos en la base. Otro carácter distintivo es que su hábito es siempre herbáceo, mientras que en los otros géneros puede ser herbáceo o leñoso.

Tabla 1. Clasificaciones taxonómicas anteriores propuestas para el género *Amaranthus* L.

Autor	Género	Subgénero	Sección	Subsección
Schinz (1934)	<i>Acnida</i> L. <i>Acanthochiton</i> Torr. <i>Amaranthus</i> L.			
Sauer (1955)	<i>Amaranthus</i>			
Aellen (1959)	<i>Amaranthus</i>	subg. <i>Amaranthus</i> subg. <i>Acnida</i>		
Robertson (1981)	<i>Amaranthus</i>	subg. <i>Amaranthus</i> subg. <i>Acnida</i> (L.) Aellen ex K. R. Robertson	secc. <i>Amaranthus</i> secc. <i>Blitopsis</i> Dumont.	
Carretero (1985)	<i>Amaranthus</i>	subg. <i>Amaranthus</i>	secc. <i>Amaranthus</i> secc. <i>Blitopsis</i> secc. <i>Pyxidium</i> Moq.	
Eliasson (1988)	<i>Amaranthus</i>	subg. <i>Amaranthus</i> subg. <i>Acnida</i>		
Mosyakin & Robertson (1996)	<i>Amaranthus</i>	subg. <i>Amaranthus</i> subg. <i>Albersia</i> (Kunth) Gren. & Godr. subg. <i>Acnida</i>	secc. <i>Amaranthus</i> nothosecc. <i>Dubia</i> Mosyakin & K. R. Robertson secc. <i>Centrusa</i> Griseb. secc. <i>Blitopsis</i> secc. <i>Goerziella</i> (Urb.) Mosyakin & K. R. Robertson secc. <i>Pentamorion</i> (Beck.) Mosyakin secc. <i>Pyxidium</i> secc. <i>Acnida</i> secc. <i>Acanthochiton</i> (Torr.) Mosyakin & K. R. Robertson secc. <i>Saueranthus</i> Mosyakin & K. R. Robertson	subsecc. <i>Amaranthus</i> subsecc. <i>Hybrida</i> Mosyakin & K. R. Robertson
Costea et al. (2001a)	<i>Amaranthus</i>	subg. <i>Amaranthus</i> subg. <i>Albersia</i> subg. <i>Acnida</i>		
Mosyakin & Robertson (2003)	<i>Amaranthus</i>	subg. <i>Amaranthus</i> subg. <i>Albersia</i> subg. <i>Acnida</i>	secc. <i>Acanthochiton</i> secc. <i>Acnida</i> secc. <i>Saueranthus</i>	

CLAVE PARA LOS GÉNEROS DE LA SUBTRIBU AMARANTHINAE
(ADAPTADO DE TOWNSEND, 1993: 21).

1. Flores estériles modificadas, ubicadas conjuntamente con las fértiles, transformadas en alas, escamas, espinas, pelos o cerdas 2

1'. Flores estériles modificadas ausentes 4

2(1). Flores estériles transformadas en escamas con venación en forma de asta de venado o ampliamente aladas y nervadas 3

2'. Flores estériles sin las formas mencionadas en 2 *Neocentema* Schinz
- 3(2). Hierbas anuales con estilos delgados y estigmas lineares *Digera* Forssk.

3'. Hierbas perennes, subarbustos o pequeños arbustos con estilo breve y un estigma cortamente bilobado ... *Pleuropterantha* Franch.

4(1'). Flores imperfectas, con las flores estaminadas situadas hacia el extremo de las inflorescencias o esparcidas entre las pistiladas, o plantas dioicas; sépalos glabros; filamentos estaminales libres (pseudostaminodios ausentes) *Amaranthus* L.

4'.	Flores perfectas (en <i>Charpentiera</i> Gaudich. son funcionalmente imperfectas); filamentos estaminales unidos en la base (pseudoestaminodios presentes)	5
5(4').	Fruto esférico, abayado; arbustos muy ramificados; pseudoestaminodios representados por cortos lóbulos carnosos	<i>Bosea</i> L.
5'.	Fruto no esférico, ni abayado; principalmente hierbas (sólo <i>Charpentiera</i> está representado por arbustos o árboles); pseudoestaminodios no formados por cortos lóbulos carnosos	6
6(5').	Frutos dehiscentes	7
6'.	Frutos indehiscentes	9
7(6).	Sépalos con 3 o más nervios ...	<i>Chamissoa</i> Kunth
7'.	Sépalos uninervados	8
8(7').	Flores reunidas en inflorescencias capituliformes esféricas o cilíndricas, sésiles o pedunculadas	<i>Allmania</i> R. Br. ex Wight
8'.	Flores reunidas en panojas o espigas	<i>Lagrezia</i> Moq.
9(6').	Árboles o arbustos con flores en panojas ...	<i>Charpentiera</i> Gaudich.
9'.	Hierbas con flores en espigas, o en tirsoes espiciformes o en cúlulas axilares densas ...	10
10(9').	Flores en tirsoes espiciformes largos	<i>Indobanalia</i> A. N. Henry & B. Roy
10'.	Flores en cúlulas axilares densas	11
11(10').	Semillas lisas; estigmas 2; brácteas no aquilladas; sépalos con un nervio medio delgado y dos nervios basales cortos	<i>Herbstia</i> Sohmer
11'.	Semillas con costillas concéntricas; estigmas 3; brácteas aquilladas; los 2 sépalos más externos con 3 nervios gruesos, mientras que los 3 internos son uninervios	<i>Siamosia</i> K. Larsen & Pedersen

MATERIALES Y MÉTODOS

El estudio se basó en el exámen de materiales de herbario y de imágenes provenientes de las principales instituciones, las cuales están abreviadas según el Index Herbariorum (Holmgren et al., 1990; Apéndice 1). Los siguientes herbarios brindaron material para su estudio en carácter de préstamo o bien fueron visitados: AAU, B, BA, BAB, CORD, CTES, GH, K, LIL, LP, LPAG, MO, NBG, NSW, NY, S, SGO, SI, US y Z. Por su parte, otras instituciones colaboraron con el envío de imágenes y asesoramiento: BISH, BM, BOLO, CAS, EA, G, HAL, LINN, LY, M, MEL, MICH, OXF, P, PH, PR, TEX, UC y UPS. Se estudiaron ejemplares de herbario de la mayor parte de las especies tratadas, con excepción de una especie americana (*Amaranthus viscidulus* Greene) y de cinco especies australianas (*A. centralis* J. Palmer & Mowatt, *A. clementii* Domin, *A. grandiflorus* (J. M. Black) J. M. Black, *A. induratus* J. Palmer & Mowatt y *A. rhombeus* R. Br.), para cuyo tratamiento se emplearon imágenes digitales. Las observaciones morfológicas se hicieron con un

microscopio binocular Nikon (Nikon, Tokio). Los aspectos morfológicos de las brácteas florales, flores y frutos fueron ilustrados por el autor con el auxilio de un microscopio binocular Wild M8 equipado con cámara clara, mientras que el hábito fértil fue dibujado por la ilustradora científica María Alejandra Migoya, quien además se encargó de pasar a tinta los detalles florales y del procesamiento digital de las imágenes. Las observaciones microscópicas de epidermis y pelos se hicieron con microscopio óptico Leitz SM (Leica, Wetzlar, Alemania) lux provisto de cámara clara.

ASPECTOS MORFOLÓGICOS

HÁBITO

Amaranthus se compone de hierbas anuales; cuatro especies sin embargo se comportan, a veces, como perennes de corta vida: *Amaranthus blitum*, *A. deflexus* L., *A. muricatus* (Moq.) Hieron. y *A. viridis* L., y tres especies como perennes, con la base del tallo leñosa: *A. peruvianus* (Schauer) Standl., *A. rosengurtii* y *A. vulgatissimus* Speg. Pueden ser plantas monoicas (*Amaranthus* subg. *Amaranthus* y *Amaranthus* subg. *Albersia*) o dioicas (*Amaranthus* subg. *Acnida*), glabras o pubescentes, de color verde, aunque a menudo con tonalidades de color rojizo debido a la presencia de betalaínas. Los haces vasculares están rodeados por una vaina parenquimática de células de forma cúbica, exhibiendo una anatomía tipo kranz, presentando caracteres morfológicos y fisiológicos de las plantas con estrategia fotosintética C₄ (Cronquist, 1981; Esau, 1982; Costea & Tardif, 2003a).

TALLO

Los tallos pueden ser variables en su longitud (desde unos pocos centímetros hasta más de 2.5 m de altura), como también en su diámetro, patrón de ramificación y color, dependiendo todos estos rasgos con frecuencia de factores ambientales. Predominan los tallos erectos o ascendentes, aunque también los hay decumbentes (e.g., *Amaranthus acutilobus* Uline & W. L. Bray, *A. crassipes* Schltdl., *A. dinteri* Schinz) o postrados (*A. furcatus* J. T. Howell, *A. hunzikeri* N. Bayón, *A. looseri* Suess., *A. minimus*), son simples o usualmente ramificados desde la base, por lo general sin espinas o excepcionalmente con un par de espinas en la base de la hoja (*A. spinosus* L.), algunas veces estriados (*A. cuspidifolius* Domin) y otras carnosos (*A. californicus* S. Watson, *A. pumilus* Raf.). Las trazas foliares son más complejas en *Amaranthus* subg. *Amaranthus* pues cuentan con nueve a 11 haces vasculares, mientras que son más

simples en *Amaranthus* subg. *Albersia* pues tienen tres a cinco (raramente siete) haces vasculares (Costea & DeMason, 2001). Tal como en el resto de *Amaranthaceae*, *Amaranthus* posee raíces y tallos con estructura anómala o atípica, a la que Metcalfe y Chalk (1989) designaron como floema interxilemático (o floema incluido). Básicamente consiste en bandas de floema sumidas en el xilema secundario del tallo o raíz. En sección transversal, las bandas pueden verse esparcidas sin ordenamiento alguno, o bien ordenadas en anillos concéntricos.

TRICOMAS

Los tricomas de los tallos son similares a los presentes en las hojas, esto es uniseriados, o a veces se observan conjuntamente multiseriados y uniseriados. Los tricomas uniseriados son glandulares, con la base unicelular o pluricelular, siendo su célula apical redondeada y un tanto mayor que las restantes. En las hojas suelen presentarse junto a papilas sobre las principales venas de la cara abaxial (Fig. 1).

HOJAS

La forma de la lámina es comúnmente rómbica, ovada, obovada, lanceolada u oblonga, y algunas veces orbicular, linear o espatulada. Su consistencia es herbácea, raramente carnosa (*Amaranthus pumilus*, *A. viscidulus*). La base puede ser atenuada, cuneada o redondeada, el margen usualmente entero y plano, rara vez ondulado (*A. californicus*, *A. capensis* Thell., *A. crispus* (Lesp. & Thévenau) J. M. Coult. & S. Watson) y el ápice agudo, obtuso, redondeado, truncado, retuso, emarginado o escotado, con la vena media a menudo prolongada en un mucrón.

INFLORESCENCIAS

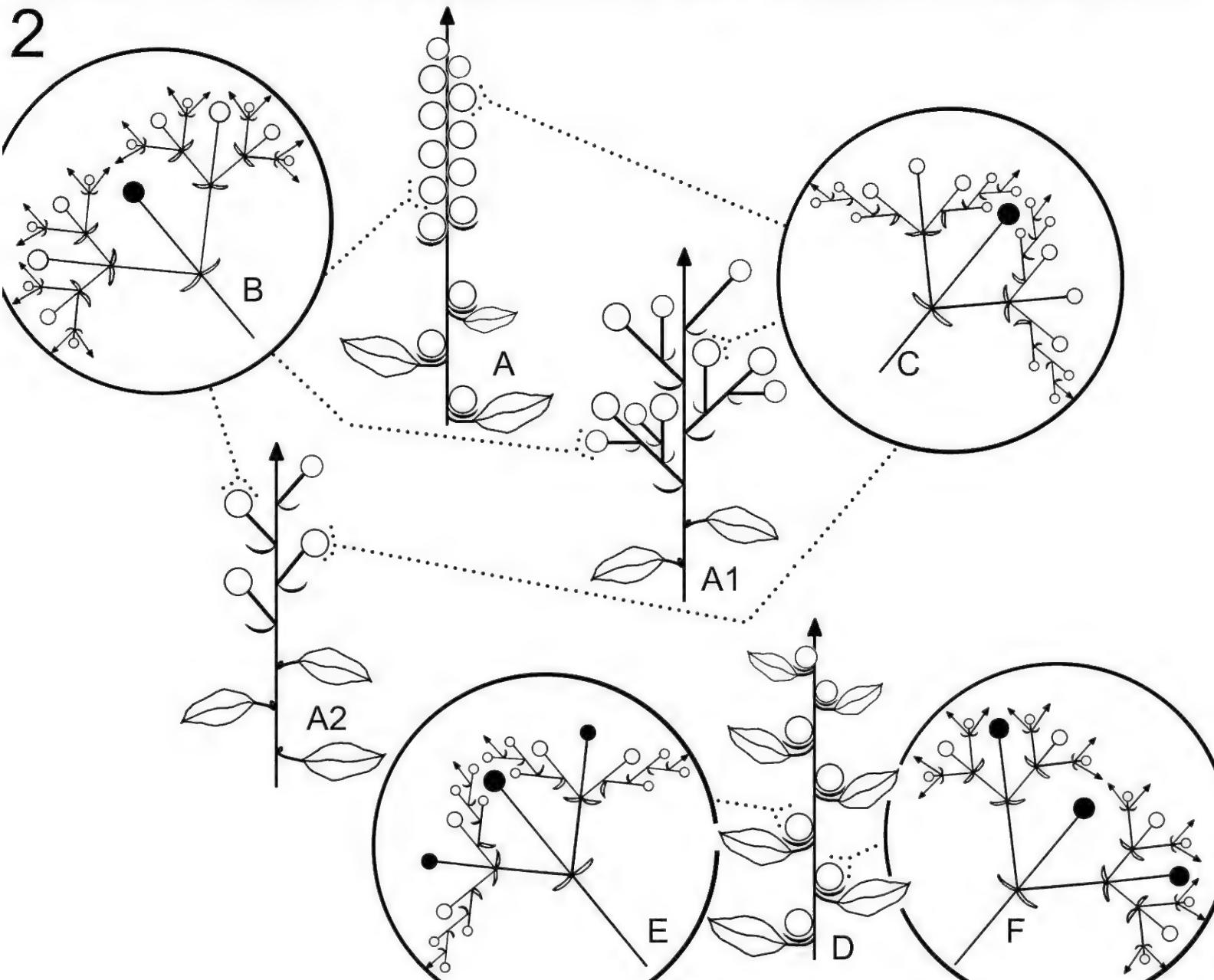
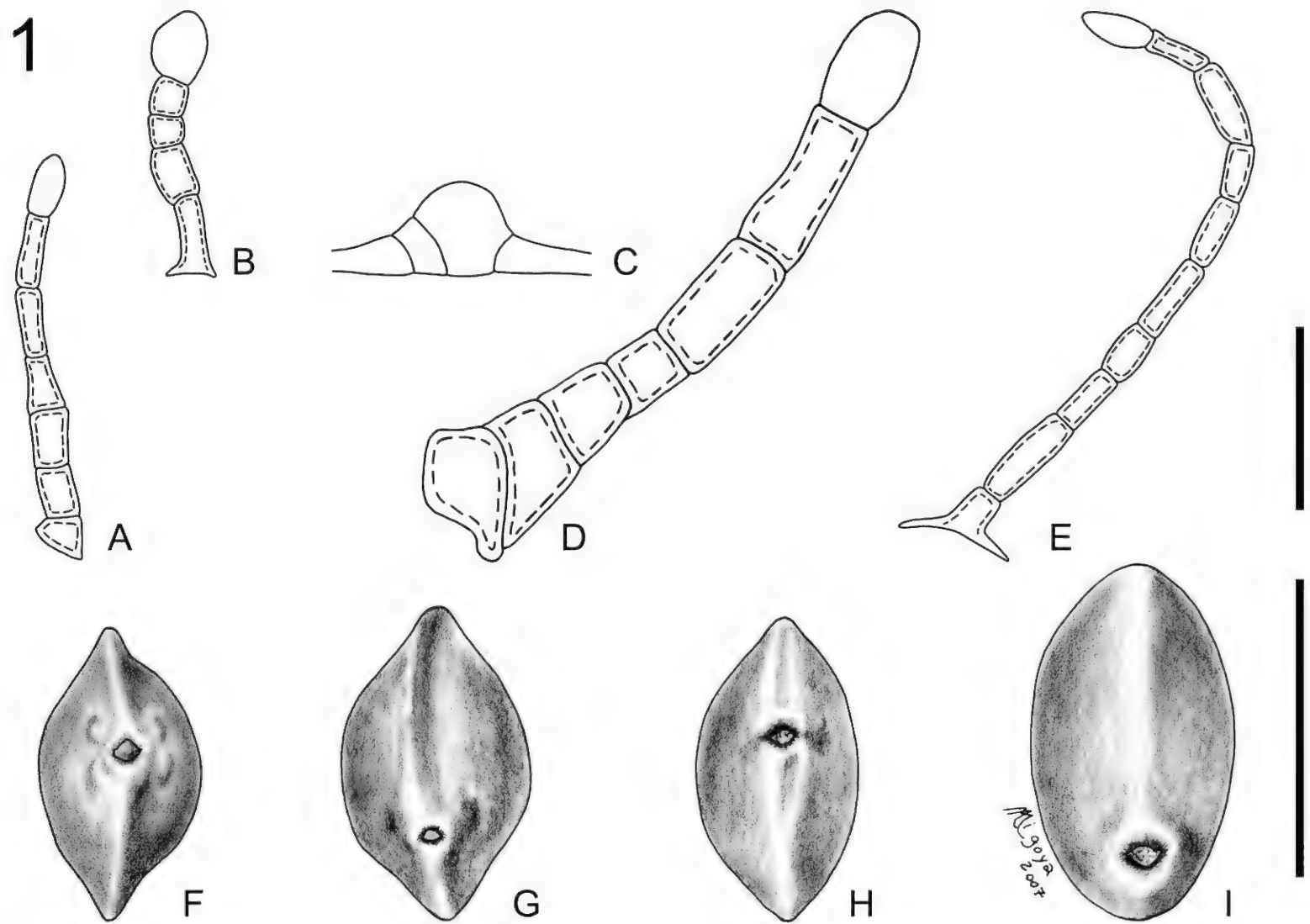
Las inflorescencias generales pueden ser predominantemente terminales, en forma de tirso, panículoide o espiciforme (*Amaranthus* subg. *Amaranthus*) (Rúa, 1999). Estas inflorescencias mayores están

constituidas a su vez por otras unidades menores o glomérulos. Otra alternativa, es que prevalezcan las inflorescencias axilares en forma de glomérulos (*Amaranthus* subg. *Albersia*). Si bien ambos tipos de inflorescencias, terminales y axilares, pueden estar presentes sobre una misma planta, tiende a predominar una u otra ubicación en cada uno de los subgéneros. La estructura de cada glomérulo es similar para todas las especies de *Amaranthus* (Fig. 2). Un glomérulo es un dicasio (o cima bípara) multifloro, en donde la primera flor tiene una posición terminal en la rama, y en su base a partir de las axilas de los dos hipsofilos, desarrollan a cada lado (en forma opuesta o subopuesta) la segunda y tercera flor sobre ramitas secundarias, sobrepasando en longitud a la rama madre. Esas dos últimas flores se transforman a su vez en terminales, y en la base de cada una desarrollan dos nuevas flores sobre las ramitas terciarias (Fig. 2B, F). Según Pal (1972) este patrón simétrico se repite sin alteraciones indefinidamente en *A. caudatus* L., mientras que en varias otras especies (e.g., *A. hypochondriacus* L., *A. tricolor* L.) existe una gradual transición que pasa de dicasio a monocasio (Fig. 2C, E). En éste último tipo de inflorescencia, la yema de uno de los dos perfiles permanece estéril. El momento en que se produce el cambio de dicasio a monocasio depende de la especie. La consecuencia en la morfología, es que en los dicasios los glomérulos resultan con una forma redondeada, mientras que en los casos en los que se produce un cambio a monocasio los glomérulos poseen una forma más alargada. La primera flor de cada glomérulo es estaminada y las restantes son pistiladas en *Amaranthus* subg. *Amaranthus*. Por el contrario, si bien la primera flor del glomérulo es también estaminada en *Amaranthus* subg. *Albersia*, entre las flores pistiladas subsiguientes se entremezclan algunas otras estaminadas. En consecuencia, la proporción de flores masculinas es mayor en el segundo subgénero que en el primero. Según lo antedicho, flores estaminadas y pistiladas ocurren en el mismo glomérulo, aunque existen casos excepcio-

→

Figura 1. Pelos representativos de *Amaranthus* L. —A. Pelo glandular de *A. deflexus* L. —B. Pelo glandular de *A. viridis* L. —C. Papila de *A. viridis*. —D. Pelo glandular de *A. retroflexus* L. —E. Pelo glandular de *A. hybridus* L. subsp. *quitensis* (Kunth) Costea & Carretero. A, ilustrado de Bayón 625 (LPAG); B, C, de Bayón 603 (LPAG); D, de Gonzalo 6889 (SI); E, de Bayón 642 (LPAG). Las barras de escala para A–E = 100 µm. Semillas representativas de *Amaranthus*. —F. Vista hilar de *A. sclerantoides* (Andersson) Andersson. —G. Vista hilar de *A. deflexus*. —H. Vista hilar de *A. graecizans* L. —I. Vista hilar de *A. crassipes* Schltld. F, ilustrado de Stewart 1360 (SI); G, de Kiesling 6672 (SI); H, de Gonzalo 6873 (SI); I, de Johnston 7076 (SI). Las barras de escala para F–I = 1 mm.

Figura 2. Inflorescencias. *Amaranthus* L. subg. *Amaranthus*. —A. Glomérulos dispuestos en inflorescencias espiciformes. —A₁. Glomérulos dispuestos en inflorescencias panículoideas. —A₂. Glomérulos dispuestos en tirsos. —B. Esquema de un dicasio. —C. Esquema de un dicasio transformándose en monocasio. *Amaranthus* subg. *Albersia* (Kunth) Gren. & Godr. —D. Rama con glomérulos axilares. —E. Esquema de un dicasio transformándose en monocasio. —F. Esquema de un dicasio. (●) Flores estaminadas; (○) flores pistiladas.



nales en que esto no es así. En ellos las flores de ambos sexos se dan en cimas separadas, como en *A. dubius* (con menor constancia), *A. minimus* y *A. spinosus*. Cada cima se dispone en la axila de una bráctea, y en algunas especies los glomérulos (componentes de inflorescencias generales) se disponen en la axila de hojas reducidas, denominadas pseudobracteas (e.g., *A. squamulatus* (Andersson) B. L. Rob., *A. tamaulipensis* Henrickson, *A. torreyi* (A. Gray) S. Watson). A veces, se da el caso en que los ejes de los dicasios se engrosan (e.g., *A. crassipes*, *A. furcatus* y *A. scleropoides* Uline & W. L. Bray).

BRÁCTEAS Y BRACTÉOLAS FLORALES

En *Amaranthus* las brácteas y bractéolas florales son fácilmente confundidas con las piezas del perianto. Tamaño, forma, y principalmente su longitud relativa al ser comparada con la de los sépalos, son caracteres valiosos para distinguir a las distintas especies. Cada flor individual está sub-tendida basalmente por una bráctea y por dos bractéolas (aunque también puede darse la presencia de una, tres, cuatro o bien estar ausentes). A veces, cada bractéola puede constituirse en bráctea floral de dos nuevas flores laterales, formándose así una címula, caso en el cual esas dos flores laterales carecen de bractéolas, y como resultado quedan entonces sostenidas por una única bráctea (Eliasson, 1988); brácteas y bractéolas florales pueden presentar diversas formas, a saber: ovadas, lanceoladas, lineares, subuladas, deltoides, elípticas u orbiculares. De acuerdo a lo establecido por Costea y Tardif (2003a) las brácteas pueden ser clasificadas en *espinosas*, *foliáceas* o *membranáceas*. En su anatomía las *espinosas* muestran una vena media rodeada por esclerénquima y parénquima, y dos alas laterales de una consistencia membranacea formadas por una capa de células. El esclerénquima predomina sobre el parénquima, por lo que tienen una consistencia rígida. Este tipo de brácteas es característico de *Amaranthus* subg. *Amaranthus*. En contraposición, las brácteas *foliáceas* no tienen una distinción tan marcada entre los tejidos de la vena media y las alas, que son angostas (e.g., *A. blitoides* S. Watson). En estas el parénquima predomina sobre el esclerénquima. Finalmente, las brácteas *membranáceas* recuerdan a las foliáceas, aunque el parénquima está apenas desarrollado, restringido a la vena media y a veces formado por tan solo una capa de células (e.g., *A. crispus*). El esclerénquima está poco desarrollado y el resto de la bráctea es delgado y membranaceo. Los dos últimos tipos mencionados son característicos de *Amaranthus* subg. *Albersia* y se dan formas inter-medias entre ambos.

En el mismo trabajo, Costea y Tardif (2003a) concluyen que las dos espinas que *Amaranthus spinosus* presenta en la base de cada hoja no son más que las bractéolas metamorfoseadas de la primer flor del primer dicasio, cuyo desarrollo se aborta. En un principio las espinas tienen un desarrollo similar al de las bractéolas, con la diferencia que en las espinas las células parenquimáticas (que se convertirán en esclerenquimáticas) se expanden unas cinco veces. La porción de las alas no se desarrolla, o lo hace ínfimamente. Las brácteas y bractéolas florales cumplen una doble función: fotosíntesis y protección. Es indudable que al ser hojas modificadas su función original es la de fotosíntesis, a la que se agrega la de protección contra los herbívoros. Aparentemente existiría una correlación entre la presencia de brácteas espinosas y la dehiscencia de los frutos: las especies con frutos dehiscentes tienen brácteas espinosas, mientras que las especies con frutos indehiscentes tienen brácteas membranáceas o foliáceas.

FLOR

Las flores son pequeñas, monoclamídeas, imperfectas, verdosas, generalmente con el mismo número de sépalos en las flores pistiladas que en las estaminadas, aunque a veces puede diferir (e.g., *Amaranthus asplundii* Thell., *A. blitum*, *A. peruvianus*). Rara vez se dan flores estériles. Algunos autores (e.g., Townsend (1985), Costea y Tardif (2003a), Mosyakin y Robertson (2003), llaman a los segmentos del perianto tépalos y no sépalos. Para Font Quer (2001) los tépalos son antofilos del perigonio, siendo este último término empleado en su acepción moderna para designar a un perianto homoclamídeo, esto es cuando no hay diferencia entre cáliz y corola. Dado que la flor del género *Amaranthus* presenta un solo ciclo de protección (flor monoclamídea) de color verde, corresponde llamarlo cáliz y a sus piezas sépalos.

FLOR PISTILADA

Las flores pistiladas están protegidas por tres a cinco sépalos (rara vez pueden estar ausentes o estar presentes tan solo uno o dos), por lo general en número constante, aunque algunas veces variable dentro de una misma especie o inclusive dentro de una misma planta (e.g., *Amaranthus asplundii*), frecuentemente libres, o más raramente connados en la base (e.g., *A. anderssonii* J. T. Howell, *A. urceolatus* Benth.), más o menos iguales entre sí (e.g., *A. cuspidifolius*, *A. fimbriatus* S. Watson, *A. standleyanus* Covas) o los externos mayores que los internos (e.g., *A. asplundii*, *A. blitoides*, *A. capensis*), por lo general de consistencia membranacea o

escariosa al madurar, raramente herbácea (e.g., *A. capensis*), glabros o rara vez con escasos y breves pelos en los bordes; con la vena media débil a marcada, simple o ramificada, a menudo excurrente en un mucrón, a veces con tres venas longitudinales, las dos laterales apenas divergentes (e.g., *A. anderssonii*, *A. polygonoides* L.). La morfología de los sépalos y su relación en tamaño con la bractéola y el fruto, brinda los caracteres más valiosos para la identificación de las especies. La flor pistilada carece de estambres, cuenta con un único pistilo formado por dos o tres carpelos; el estilo por lo general es corto o a veces está ausente y los estigmas son dos o tres, delgados, subulados y persistentes, de posición extendida o recurvada. Hay un óvulo, de tipo campilótropo, sostenido por un funículo breve, con micrópilo inferior.

FLOR ESTAMINADA

Las flores estaminadas tienen tres a cinco sépalos (rara vez uno o dos), iguales o subiguales; los estambres se presentan en número de tres a cinco (rara vez uno o dos), opuestos a los sépalos, con los filamentos libres en su base. Las anteras son dorsifijas, introrsas, tetrasporangiadas, biloculares, con dos líneas de dehiscencia durante la antesis; los apéndices interestaminales (pseudostaminodios) están ausentes. El pistilo está ausente, muy rara vez rudimentario; se presentan a menudo filamentos sin sus correspondientes anteras, caso en el que son más largos que los que poseen anteras, aunque su número sumado al de estambres completos concuerda con el propio de cada especie.

FRUTO

Siguiendo los sistemas tradicionales de clasificación de frutos, en el presente tratamiento se ha considerado que el género *Amaranthus* puede presentar frutos indehiscentes, de tipo utrículo (fruto uniseminado, seco, con el pericarpio delgado no soldado a la semilla), o dehiscentes de tipo pixidio (fruto sincárpico capsular de dehiscencia transversal). El término utrículo se ajusta a la literatura americana (e.g., Judd, 1985; Spjut, 1994), mientras que también se lo ha denominado aquenio según el punto de vista europeo (e.g., Aellen, 1959; Stace, 1991). En el caso de los frutos dehiscentes, las denominaciones empleadas para designarlos han sido pixidio o cápsula uniseminada (Townsend, 1988; Stace, 1991; Costea et al., 2001b). Eliasson (1988) designa a los frutos según su dehiscencia: dehiscentes (circumscissile), irregularmente dehiscentes o indehiscentes. El fruto se halla flojamente encerrado

por los sépalos que son persistentes sobre el mismo. Algunas veces presentan venas conspicuas en número de tres y tienen forma elipsoidal, ovoide o elongada, con el pericarpio delgado, membranáceo, con la superficie lisa (e.g., *A. acutilobus*, *A. deflexus*), rugosa (e.g., *A. blitum*, *A. crispus*), tuberculada (e.g., *A. crassipes*) o formando costillas (e.g., *A. mitchellii* Benth.), por lo general glabra. Cuando son dehiscentes, es muy común que la porción basal, llamada urna, tenga la superficie lisa, mientras que la porción superior que se separa como resultado de la dehiscencia transversal, llamada opérculo, sea rugosa o tuberculada. Otro rasgo interesante, es la forma del fruto hacia la zona estigmática: el adelgazamiento puede ser gradual (e.g., *A. hypochondriacus*) o bien abrupto (e.g., *A. cruentus* L.), hasta casi truncado con la consiguiente formación de un pico (e.g., *A. crassipes*, *A. mitchellii*). La dehiscencia es un carácter empleado para la distinción de especies. Si bien se lo puede considerar constante, existen algunos casos de variabilidad dentro de una especie, población o incluso dentro de un mismo individuo (e.g., *A. hybridus*, *A. urceolatus*).

SEMILLA

Las semillas son de forma lenticular o subglobosa, de color negro o castaño oscuro en la mayor parte de las especies (e.g., *Amaranthus blitum*, *A. viridis*), o blancuzco o amarillento, a menudo con pequeñas máculas rojizas en las especies usadas como pseudocereales (e.g., *A. caudatus*, *A. cruentus* y *A. hypochondriacus*). Su tegumento es por lo general liso y brillante en las caras (área central), y generalmente reticulado o punteado en el área marginal o periférica, carente de arilo, con el embrión en forma anular, rodeando el tejido de reserva, con perisperma abundante y harinoso y endosperma escaso. Entre los caracteres de la semilla, Costea et al. (2001a) destacan la diferencia entre la posición relativa del hilo y la radícula. Según dichos autores, dada la postura vertical que adopta la semilla, ocurre que en *Amaranthus* subg. *Amaranthus* (exceptuando a *A. hybridus*) el hilo adopta una posición inferior con respecto a la radícula, mientras que por el contrario, en *Amaranthus* subg. *Albersia* la radícula llega más abajo que el hilo. De la observación de este carácter en las especies monoicas se concluye que no existe una discontinuidad en el carácter que permita separar a las especies de ambos subgéneros. Otro rasgo de la semilla es su margen visto de perfil, el que puede ser agudo (e.g., *A. albus* L., *A. persimilis*, *A. sclerantoides* (Andersson) Andersson), obtuso (e.g., *A. acutilobus*, *A. blitoides*) o redondeado (e.g., *A. brownii* Chritoph. & Caum, *A. crassipes*). Cf. Figura 1.

Tabla 2. Distribución de las especies de *Amaranthus* L. subg. *Amaranthus* y *A.* subg. *Albersia* Gren. & Godr. por continente. Las secciones son las propuestas por Mosyakin y Robertson (1996).

<i>Amaranthus</i> L.	África	América	Australia	Eurasia
subg. <i>Amaranthus</i> L.	—	13	—	—
subg. <i>Albersia</i> (Kunth) Gren. & Godr.				
secc. <i>Blitopsis</i> Dumort.	—	9	1	1
secc. <i>Goerziella</i> (Urb.) Mosyakin & K. R. Robertson	—	1	—	—
secc. <i>Pyxidium</i> Moq.	5	8	3	2
secc. <i>Pentamorion</i> (Beck) Mosyakin	—	15	7	—
Sub-totales	5	46	11	3

NÚMERO CROMOSÓMICO

Darlington y Wylie (1956) presentan el recuento de cromosomas de 13 especies, mientras que Queirós (1989) estudia cariológicamente a ocho especies del género, coincidiendo en que el número somático de cromosomas puede ser de 32 o 34 ($x = 16, 17$). Por su parte, Poggio y Greizerstein (1997), al estudiar a las tres especies empleadas como pseudocereales encuentran los mismos valores. *Amaranthus dubius* es la única especie tetraploide conocida hasta el presente dentro del género. Esta especie según Grant (1959) constituye un alopoliploide producto de la hibridación entre *A. spinosus* y probablemente *A. hybridus* subsp. *quitensis*.

POLEN

El polen fue estudiado por Costea et al. (2001a) en *Amaranthus hybridus* (*Amaranthus* subg. *Amaranthus*) y por Eliasson (1988) en *A. urceolatus* (*Amaranthus* subg. *Albersia*). Para las especies estudiadas, Costea et al. (2001a) y Eliasson (1988) mencionan un polen tipo-*Amaranthus*, encontrado también en los géneros afines *Chamissoa* y *Herbstia* y en otros géneros del nuevo mundo de la familia Amaranthaceae. El polen es pantoporado con téctum espinuloso y/o perforado. Su diámetro es pequeño, del orden de los 18–28 μm , con poros frecuentemente hundidos y la exina extraporal más o menos convexa. Los poros son usualmente más de 18 y se hallan cubiertos por pequeñas máculas granulosas o angulosas de la exina.

DISTRIBUCIÓN GEOGRÁFICA

El género *Amaranthus* es predominantemente americano, distribuyéndose desde los Estados Unidos hasta Chile y Argentina. Los dos géneros más afines, *Chamissoa* y *Herbstia*, también muestran distribución americana. El primero, con dos especies, se encuentra en América tropical y subtropical, desde México y el Caribe por toda Sudamérica hasta el norte de Argentina, no encontrándose en Chile. Por

su lado, el género monotípico *Herbstia*, se distribuye en el este de Brasil, Paraguay y el noreste de Argentina. Tanto las 13 especies de *Amaranthus* subg. *Amaranthus* como la mayor parte de las pertenecientes a *Amaranthus* subg. *Albersia*, esto es 33 especies sobre 52, son de distribución americana (Tabla 2). En América del Norte se encuentran 16 especies pertenecientes a los dos subgéneros bajo estudio. Por un lado, de *Amaranthus* subg. *Amaranthus* son cinco los representantes (*A. fimbriatus*, *A. hypochondriacus*, *A. powellii* S. Watson, *A. retroflexus* L. y *A. wrightii* S. Watson), mientras que de *Amaranthus* subg. *Albersia* son 11 (*A. acutilobus*, *A. albus*, *A. blitoides*, *A. brownii* [en rigor de Hawai], *A. californicus*, *A. obcordatus* (A. Gray) Standl., *A. pumilus*, *A. scleropoides*, *A. tamaulipensis*, *A. torreyi* y *A. viscidulus*). En América Central y el Mar Caribe se encuentran otras cinco especies (*A. cruentus*, *A. minimus*, *A. scariosus* Benth., *A. crassipes* y *A. polygonoides*—estas dos últimas también presentes en las costas australes de América del Norte). *Amaranthus cruentus* y *A. scariosus* pertenecen a *Amaranthus* subg. *Amaranthus* y las especies restantes a *Amaranthus* subg. *Albersia*. De las Islas Galápagos se conocen tres endemismos (*A. anderssonii*, *A. furcatus* y *A. sclerantoides*) y otra especie que también se halla presente en Ecuador continental (*A. squamulatus*). Son nativas de los Andes de América del Sur nueve especies, seis de *Amaranthus* subg. *Albersia* (*A. hunzikeri*, *A. kloosianus*, *A. pedersenianus* N. Bayón & C. Peláez, *A. peruvianus*, *A. persimilis* y *A. urceolatus*) y tres pertenecientes a *Amaranthus* subg. *Amaranthus* (*A. asplundii*, *A. cardenasianus* y *A. caudatus*). En el resto de América del Sur se encuentran 11 especies, de las que salvo *A. dubius* y *A. spinosus*, todas pertenecen a *Amaranthus* subg. *Albersia* (*A. crispus*, *A. deflexus*, *A. lombardoi*, *A. looseri*, *A. muricatus*, *A. rosengurtii*, *A. standleyanus*, *A. viridis* y *A. vulgatissimus*). *Amaranthus hybridus* por su parte muestra una distribución muy amplia, abarcando desde el sudeste de América del Norte hasta el centro de Argentina. Australia cuenta con 11

especies distribuidas en su continente (*A. centralis*, *A. clementii*, *A. cochleitepalus* Domin, *A. cuspidifolius*, *A. grandiflorus*, *A. induratus*, *A. interruptus* R. Br., *A. macrocarpus* Benth., *A. mitchellii*, *A. rhombus* y *A. undulatus* R. Br.), África con cinco especies (*A. capensis*, *A. dinteri*, *A. praetermissus* Brenan, *A. thunbergii* Moq. y *A. schinzianus* Thell.) y Eurasia con tres (*A. blitum*, *A. tricolor* y *A. graecizans*, esta última con un área de distribución que abarca también el norte de África). Ambos subgéneros presentan su máxima diversidad en zonas tropicales, subtropicales y templado cálidas.

TRATAMIENTO SISTEMÁTICO

Amaranthus L., Sp. Pl. 2: 989. 1753, non *Amaranthus* Adans., Fam. Pl. 269. 1763. TIPO: *Amaranthus caudatus* L.

Hierbas anuales, rara vez perennes, monoicas (*Amaranthus* subg. *Amaranthus* y *Amaranthus* subg. *Albersia*, tratadas en el presente trabajo) o dioicas (*Amaranthus* subg. *Acnida*, no tratadas en el presente trabajo), glabras o pubescentes, de color verde o rojizo. Tallos erectos, ascendentes, decumbentes o postrados, frecuentemente ramificados, a veces simples, sin espinas (salvo en *A. spinosus*). Hojas alternas, pecioladas; lámina rómbica, ovada, obovada, espatulada, lanceolada, orbicular o linear, plana o algunas veces ondulada, base atenuada, cuneada o redondeada, margen generalmente entero, ápice agudo, obtuso o emarginado, mucronulado, estípulas ausentes. Inflorescencias terminales y/o axilares, formadas por dicasios compuestos, reunidos en inflorescencias espiciformes, tirso, paniculoides o glomérulos; a veces con hojas reducidas (pseudo-brácteas) en la axila de los componentes de las inflorescencias terminales, con brácteas en la axila de los dicasios. Brácteas y bractéolas florales ovadas, lanceoladas, lineares o deltoides; bractéolas por lo general 2. Flores imperfectas, pequeñas, verdosas o rojizas, con sépalos glabros o glabrescentes. Flores pistiladas regularmente con 3 a 5 sépalos, raramente desnudas o con 1 o 2, libres o connados en la base, iguales o desiguales, siendo en este caso menores los internos, membranáceos cuando jóvenes, a veces escariosos a la madurez; estambres ausentes; un pistilo; un óvulo; estilo ausente o único; 2 o 3 estigmas, delgados. Flores estaminadas regularmente con 3 a 5 sépalos, raramente con 1 o 2, iguales o desiguales; regularmente con 3 a 5 estambres, raramente 1 o 2, filamentos libres hasta la base, anteras tetra-loculares, con 2 líneas de dehiscencia; pseudoestaminodios ausentes; pistilo ausente. Frutos uniseminados, con paredes delgadas de consistencia

membranácea, pericarpo liso o rugoso, dehiscente (píxido) o indehiscente (utrículo). Semilla una, lenticular o subglobosa, por lo general lisa, brillante, a veces reticulada o punticulada; embrión formando un anillo alrededor del perisperma, radícula inferior.

CLAVE PARA DIFERENCIAR LOS SUBGÉNEROS MONOICOS DEL GÉNERO *AMARANTHUS*

1. Inflorescencias terminales espiciformes, paniculoides o en tirso, y axilares semejantes a las terminales; brácteas y bractéolas florales espinosas; frutos dehiscentes; sépalos generalmente 5 (raramente 3 o 4); plantas erectas I. *Amaranthus* subg. *Amaranthus* L.
- 1'. Inflorescencias axilares, en glomérulos o brevemente espiciformes (a veces pueden darse inflorescencias terminales pero en ese caso los frutos son indehiscentes o bien los sépalos están en número menor a 5); brácteas y bractéolas membranáceas o foliáceas, raramente espinosas; frutos indehiscentes o dehiscentes; sépalos generalmente entre 3 y 5 (raramente 1 o 2); plantas ascendentes o postradas, raramente erectas II. *Amaranthus* subg. *Albersia* (Kunth) Gren. & Godr.

I. *Amaranthus* L. subg. *Amaranthus*, Sp. Pl. 2: 989. 1753. *Amaranthus* secc. *Amaranthotypus* Dumort., Fl. Belg. (Dumortier): 19. 1827. *Amaranthus* secc. *Euamaranthus* Moq. in de Candolle, Prodr. 13(2): 255. 1849, como “*Amarantus* secc. *Euamarantus*”, nom. inval. *Amaranthus* subg. *Euamaranthus* (Moq.) Gren. & Godr., Fl. France 3(1): 4. 1855, nom. inval. TIPO: *Amaranthus caudatus* L. Figura 3.

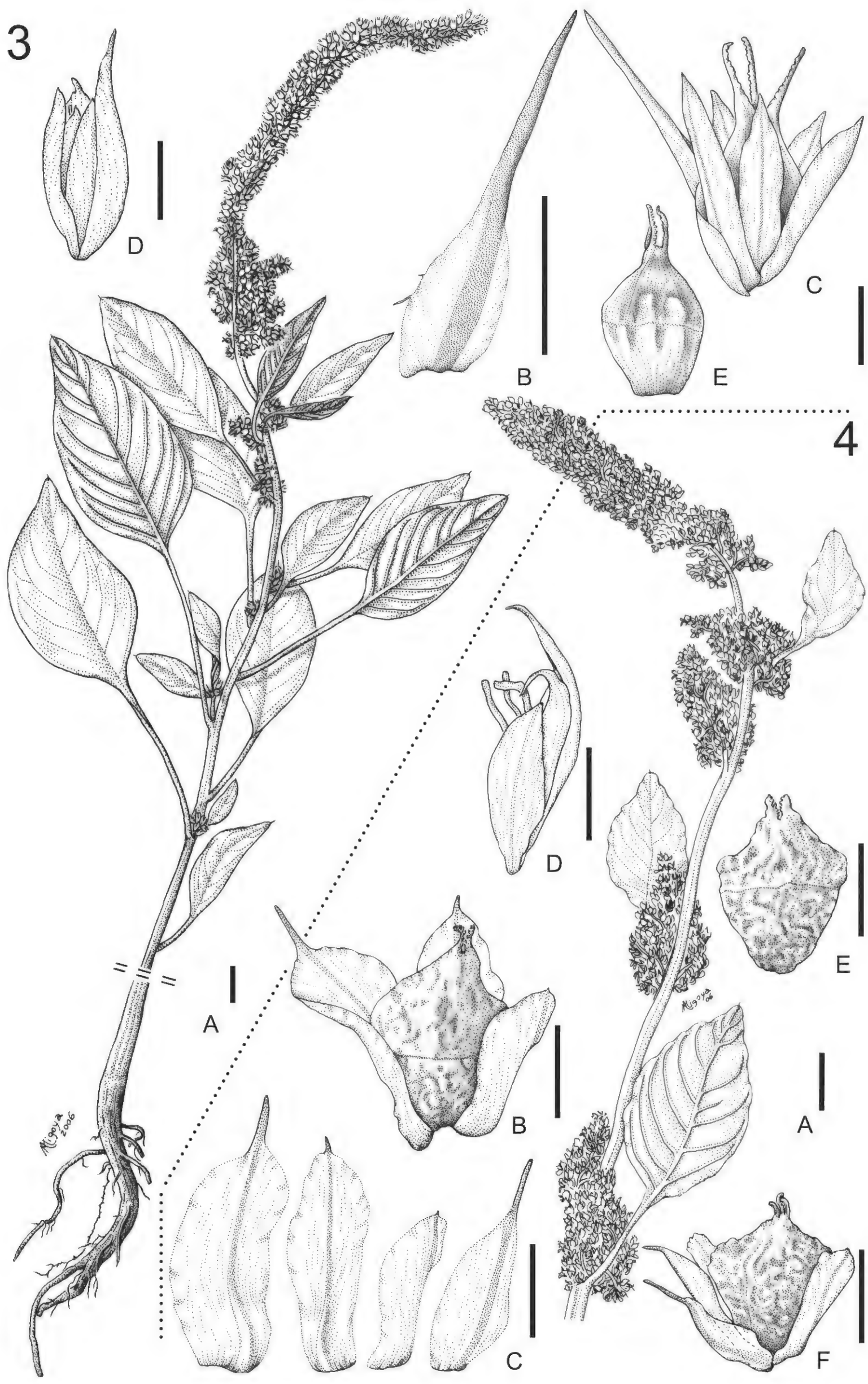
Sarratia Moq. in de Candolle, Prodr. 13(2): 233, 268–269. 1849, p.p. TIPO: *Amaranthus scariosus* Benth. [= *Sarratia scariosa* (Benth.) Moq.], lectotipo, aquí designado.

Amaranthus secc. *Centrusa* Griseb., Fl. Br. W. I. 68. 1859. *Amaranthus* secc. *Acanthophora* Beck, Icon. Fl. Germ. Helv. 24: 177. 1909, nom. illeg. superfl. TIPO: *Amaranthus spinosus* L.

Amaranthus subsecc. *Hybrida* Mosyakin & K. R. Robertson, Ann. Bot. Fenn. 33: 278. 1996. TIPO: *Amaranthus hybridus* L.

Amaranthus nothosecc. *Dubia* Mosyakin & K. R. Robertson, Ann. Bot. Fenn. 33: 278. 1996. TIPO: *Amaranthus dubius* Mart.

Hierbas anuales, monoicas. Tallos principales normalmente erectos, sólo a veces postrados o ascendentes, glabros, subglabros o pubescentes en la porción distal. Hojas pecioladas, alternas, con láminas lanceoladas, ovadas, rómbicas o elípticas, atenuadas o cuneadas en la base, generalmente con un corto mucrón apical. Inflorescencias predominantemente terminales, espiciformes, paniculoides o en tirso, aunque también en las axilas de las hojas superiores, espiciformes o en glomérulos. Brácteas y



bractéolas florales espinescentes, con la vena media rígida y con 2 alas membranáceas. Flores de ambos sexos sobre la misma inflorescencia, siendo sólo la primera flor de cada glomérulo estaminada y las restantes pistiladas. En algunas especies las flores estaminadas y las pistiladas se dan en cimas separadas (e.g., *Amaranthus dubius* y *A. spinosus*) dentro de una misma inflorescencia general. Flores estaminadas con 5 (raramente 3) sépalos y 5 (raramente 3) estambres. Flores pistiladas con 5 (raramente 3) sépalos y 3 carpelos. Frutos con dehiscencia transversal o excepcionalmente indehiscentes en algunos individuos (e.g., *A. asplundii*, *A. hybridus*, *A. powellii* y *A. spinosus*).

Etimología y ortografía. La asociación entre estas plantas y el nombre es bastante reciente. El vocablo sin embargo data de Grecia y Roma antiguas en donde ya se había usado dos mil años antes. Fue empleado por Dioscórides (4: 57, Gunther, 1959), ἀμαραντος que proviene del adjetivo ἀμόραντος (alpha privativo, maraino, marcesible), haciendo referencia a que es inmarcesible, esto es que no se puede marchitar y que las flores o inflorescencias perduran. Thellung (1919a: 225) explica que al incorporarse la palabra anthos en la etimología, el nombre debió haber sido *Amarananthus* y no *Amaranthus* (Costea & Tardif, 2003b).

El uso del nombre es anterior al siglo XVI, cuando se da la introducción de los *Amaranthus* americanos a Europa. Tampoco se conocía en Europa a la especie asiática *A. tricolor*, aunque sí a una especie a la que se le daba el nombre de “blite” cuyo nombre latino es *A. blitum*. Los antiguos griegos empleaban el nombre ἀμαραντος (amarantos) como sinónimo de elichruson (*Helichrysum* Mill., Gard. Dict. Abr., ed. 4. 1754) (Costea & Tardif, 2003b), perteneciente a la familia Asteraceae y cuyas especies son llamadas “inmortales” o “siemprevivas” (de la Peña & Pensiero, 2004), haciendo referencia a sus filarios inmarcesibles. Por su parte Plinio el Viejo parece referirse con el nombre ἀμαραντος (amarantos) a otra planta perteneciente en este caso a la familia Amaranthaceae: *Celosia argentea* L. (*Celosia*, Sp. Pl. 205. 1753). El que hace válidas las diferencias

entre los géneros *Celosia* y *Amaranthus* es Linneo en 1753.

La forma Latina adoptada por Plinio el Viejo fue *amarantus* (1951 [traducción]: 41), siendo *amarantus* la forma supuestamente incorrecta, resultado de no haberse respetado la etimología. Sprague (1928) dirime esta cuestión al sostener que el punto central no está en el uso correcto de la ortografía, sino en si el nombre genérico *Amaranthus* L. (1753) está de acuerdo o no con el Código Internacional de Nomenclatura (McNeill et al., 2012). Con anterioridad a 1753, los distintos autores usaron una y otra forma. Linneo conocía las dos ortografías de la palabra y deliberadamente escogió *Amaranthus* en detrimento de *Amarantus*. Por lo tanto, de acuerdo a las reglas del Código (Art. 60, McNeill et al., 2012), debe considerarse como correcta a la primera de esas variantes ortográficas, aunque se oponga a la ortografía clásica de la palabra.

Discusión. Según Moquin (1849) la sección *Euamaranthus* cuenta con 15 especies. Nueve de esos nombres se corresponden con taxones de *Amaranthus* subg. *Amaranthus*, dos a taxones de *Amaranthus* subg. *Albersia*, siendo los cuatro restantes de identidad dudosa. Los nombres de las especies de la sección *Euamaranthus* propuesta por Moquin (1849) son los que siguen a continuación: *A. anardana* Buch.-Ham., *A. caracasanus* Kunth, *A. caudatus*, *A. celosioides* Kunth, *A. chlorostachys* Willd., *A. flavus* L., *A. gangeticus* L., *A. hybridus*, *A. hypochondriacus*, *A. mangostanus* L., *A. paniculatus* L., *A. retroflexus*, *A. speciosus* Sims., *A. spinosus* y *A. tristis* L. Mientras que cinco de esos nombres se corresponden con los nombres incluidos en *Amaranthus* subg. *Amaranthus* del presente tratamiento (*A. caudatus*, *A. hybridus*, *A. hypochondriacus*, *A. retroflexus* y *A. spinosus*), otros cuatro son aquí contemplados como sinónimos de especies de ese subgénero, a saber: *A. anardana* es aquí incluido como sinónimo de *A. hypochondriacus*; *A. flavus* y *A. paniculatus* como sinónimos de *A. cruentus*, y *A. chlorostachys* como sinónimo de *A. hybridus*. Los nombres *A. mangostanus* y *A. tristis* son aquí considerados como sinónimos de *A. tricolor*, perteneciente al otro subgénero tratado, *Amaranthus*

Figura 3. Lámina general de *Amaranthus* L. subg. *Amaranthus*. —A. Planta de *A. caudatus* L. —B. Bráctea espinescente de *A. caudatus*. —C. Flor pistilada de *A. hypochondriacus* L. —D. Flor estaminada de *A. retroflexus* L. —E. Fruto de *A. cruentus* L. A, ilustrado de Schimper 1535 (GH); B, de Burkart 17809 (SI); C, de Powell s.n. (NY); D, de Bayard Long 61638 (SI); E, de Tuerckheim 8567 (K). La barra de escala para A = 1 cm; para B–E = 1 mm.

Figura 4. *Amaranthus asplundii* Thell. subsp. *asplundii*. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. *Amaranthus asplundii* subsp. *australis*. (Hunz.) N. Bayón. —F. Flor pistilada. A, ilustrado de Asplund 3838 (Z); B–D, de Asplund 4071 (Z); E, de Asplund 3838 (S); F, de Hunziker 2574 (CORD). La barra de escala para A = 1 cm; para B–F = 1 mm.

subg. *Albersia*. Finalmente, *A. celosioides*, *A. caracasanus*, *A. gangeticus* y *A. speciosus* constituyen taxones dudosos.

Moquin (1849) al describir *Sarratia* menciona las siguientes tres especies: *S. urceolata* Moq., *S. berlandieri* Moq. y *S. scariosa* Moq. Los caracteres observados en los materiales tipo y la diagnosis de *S. scariosa* se corresponden con *Amaranthus* subg. *Amaranthus*, mientras que los de *S. berlandieri* y *S. urceolata* se corresponden con *Amaranthus* subg. *Albersia*. Dado que en la diagnosis del género *Sarratia* se hace mención a que las flores estaminadas poseen cinco estambres y a que los frutos son dehiscentes, caracteres propios de *S. scariosa* pero no de las otras dos, se opta por designar a *S. scariosa* como lectotipo del género.

CLAVE PARA LA DIFERENCIACIÓN DE LAS ESPECIES (13) DE
AMARANTHUS SUBG. *AMARANTHUS*

1. Sépalos en número variable de (0 o 1 o)3 a 5, por lo general muy desiguales entre sí 1. *A. asplundii* Thell.

1'. Sépalos siempre en número de 5 2

2(1'). Hojas lineares o linear-lanceoladas 6. *A. fimbriatus* (Torr.) Benth. ex S. Watson

2'. Láminas nunca lineares, ni linear-lanceoladas 3

3(2'). Hojas con espinas apareadas en la base del pecíolo 12. *A. spinosus* L.

3'. Hojas sin espinas en la base del pecíolo 4

4(3'). Inflorescencias terminales con cimas superiores exclusivamente estaminadas y las basales exclusivamente pistiladas (a veces puede haber alguna flor estaminada entre las pistiladas) 5. *A. dubius* Mart. ex Thell.

4'. Inflorescencias terminales con flores estaminadas esparcidas entre las flores pistiladas 5

5(4'). Brácteas y bractéolas florales generalmente más cortas que los sépalos 2. *A. cardenasianus* Hunz.

5'. Brácteas y bractéolas florales iguales o mayores que los sépalos 6

6(5'). Inflorescencias grandes y robustas cuando plenamente desarrolladas, mayores de 30 cm, por lo general de colores vivos, rojo, púrpura, a veces blanco o amarillento, raramente verdes; semillas de color blanco, marfil, rojizo, castaño o negro; plantas cultivadas, rara vez escapadas de cultivo 7

6'. Inflorescencias moderadamente grandes, generalmente menores de 30 cm (sólo a veces *A. scariosus* puede superar ese tamaño), de color verde o rojizo; semillas de color castaño o negro; plantas espontáneas 9

7(6). Inflorescencias rígidas, erectas; frutos adelgazándose en forma gradual hacia la zona estigmática, formando un pico evidente con arrugas; brácteas y bractéolas florales 3–6(–8) mm 8. *A. hypochondriacus* L.

7'. Inflorescencias flácidas, péndulas (raramente erectas); frutos adelgazándose gradual
- o abruptamente hacia la zona estigmática; brácteas y bractéolas florales 2–4 mm 8

8(7'). Sépalos de las flores pistiladas oblongos a lanceolados, agudos; ramas estigmáticas erectas o apenas reflejas; inflorescencia no caudada, con sus ramas basales desarrolladas; frutos adelgazándose abruptamente hacia la zona estigmática formando un pico corto y liso; brácteas y bractéolas florales 2–3 mm 4. *A. cruentus* L.

8'. Al menos los sépalos internos de las flores pistiladas espatulado-obovados u oblongo-obovados, obtusos o emarginados; ramas estigmáticas divergentes o reflejas; inflorescencia caudada, con sus ramas basales poco o nada desarrolladas; frutos adelgazándose gradualmente hacia la zona estigmática, sin pico; brácteas y bractéolas florales 3–4 mm 3. *A. caudatus* L.

9(6'). Sépalos de las flores pistiladas obtusos, redondeados o emarginados en el ápice 10

9'. Sépalos de las flores pistiladas con el ápice agudo 12

10(9). Tallos densamente pubescentes, sobre todo cerca de la inflorescencia; sépalos de las flores pistiladas con la vena media terminando por debajo del ápice 10. *A. retroflexus* L.

10'. Tallos glabros o casi glabros; la vena media de los sépalos de las flores pistiladas llega hasta el ápice de los mismos 11

11(10'). Bractéolas que llegan a duplicar en longitud a los sépalos; sépalos de las flores pistiladas 1.5–2 mm, oblongos, oblongo-espatulados u oblongo-obovados 13. *A. wrightii* S. Watson

11'. Brácteas y bractéolas florales apenas más largas que los sépalos; sépalos de las flores pistiladas 2.3–3 mm, obovados o espatulados 11. *A. scariosus* Benth.

12(9'). Brácteas y bractéolas florales de 2–4 mm; inflorescencia usualmente laxa, flexible, con ramas que se separan del eje principal ... 7. *A. hybridus* L.

12'. Brácteas y bractéolas de 4.5–6(–8) mm; inflorescencia usualmente rígida, con ramas erectas cercanas al eje principal 9. *A. powellii* S. Watson

I. 1. *Amaranthus asplundii* Thell., Repert. Spec. Nov. Regni Veg. 21: 322. 1925. TIPO: Bolivia. Cochabamba: Prov. Cercado, Cochabamba, ca. 2500 m, 8 jun. 1921, *E. Asplund* 4071 (lectotipo, aquí designado, S-03-252 no visto, imagen!; isotipos, S-07-8954 no visto, imagen!, UPS no visto, imagen!; isotipo, Z [código de barras] Z000000237!). Figura 4.

Hierba anual; tallos principales postrados, radiados, muy ramificados, algunas veces ascendentes, 0.15–0.50 m, frecuentemente con tonalidades rojizas, subglabros, puberulentos o escasamente pubescentes cerca de las inflorescencias cuando jóvenes. Hojas con pecíolo 1.2–3 cm, glabras o glabrescentes en el

margen cuando jóvenes, lámina elíptica, ovado-rómbica u oblonga, no ondulada, $1-5 \times 0.8-3$ cm, cuneada o atenuada en la base, obtusa a retusa en el ápice, a menudo con el margen rojizo, mucrón 1.2 mm. Inflorescencias terminales o axilares, las primeras en panojas de ramificaciones breves, o espiciformes, alargadas, de 8×1 cm, las segundas más o menos redondeadas, de color verde o rojizo; brácteas y bractéolas ovadas, 2–3 mm, más cortas o casi de la longitud de los sépalos, espinescentes, naviculares, reflejas, con arista de 0.5–1 mm. Flores de ambos sexos sobre la misma inflorescencia. Flores estaminadas con 3(5) sépalos lanceolados, 1.5–2.5 mm, agudos, membranáceos, desiguales entre sí, blancuzcos con la vena media de color verdoso, 3(5) estambres. Flores pistiladas con (0 o 1)2 a 5 sépalos muy desiguales entre sí: el externo oblongo a oblongo-elíptico, de hasta 3 mm, mucronado, mucrón 0.2–0.8 mm; los internos angostamente elípticos u oblongo-elípticos, de hasta 1.5 mm; estigmas 2 o 3, de hasta 0.5 mm, delgados, por lo que se quiebran con facilidad. Frutos dehiscentes o indehiscentes, completamente o al menos con el opérculo rugoso, no tan largos como el sépalo mayor, aunque sí más largos que los restantes; semillas de color castaño-rojizo a negro, 1.3×1.1 mm, brillantes en el centro, con escultura en el margen.

Distribución y ecología. *Amaranthus asplundii* es nativa de las zonas altas de América del Sur desde Ecuador hasta Chile y noroeste de Argentina (Eliasson, 1987; Pedersen, 1994). Esta especie crece en lugares húmedos y sombreados, a veces cerca de viviendas, sobre terraplenes de ferrocarril y en cultivos de maíz. Se distribuye entre los 1600 y los 3400 m (Barboza et al. 1465, 1466, CORD; Hunziker, 1966; Carrizo & Isasmendi, 1998). Florece y fructifica en los meses de febrero a mayo.

Discusión. Esta especie es muy característica por el número variable de sépalos en sus flores pistiladas y por la diferencia existente entre ellos, por lo que no se la encuentra semejante a ninguna de sus congéneres.

Thellung (1925) describe *Amaranthus asplundii* sobre la base del material *Asplund 4071*, del cual existen dos ejemplares depositados en S, uno en UPS y otro en Z. Mientras que los tres primeros constan de porciones de plantas con abundantes hojas e inflorescencias, el último (del que ha sido posible su estudio) posee un fragmento de tallo con unas pocas hojas y una pequeña inflorescencia. De todos ellos se designa como lectotipo de *A. asplundii* al ejemplar S (S-03-252) por estar en un todo de

acuerdo con el protólogo y presentar numerosas hojas e inflorescencias bien desarrolladas.

CLAVE PARA LA DIFERENCIACIÓN DE LAS SUBESPECIES DE
AMARANTHUS ASPLUNDII

1. Cuando el número de sépalos es 3, el sépalo mayor es comparativamente ancho, 1.9–2.8(–3.2) mm (incluido el largo mucrón de 0.2–0.8 mm), igualando o superando el ápice de los estigmas; ovario claramente oblongo *A. asplundii* Thell. subsp. *asplundii*
- 1'. Cuando el número de sépalos es 3, el sépalo mayor es comparativamente angosto, 1.5–2.2(–2.4) mm (incluido el breve mucrón de 0.1–0.2 mm), igualando al ovario fructificado o la base de los estigmas; ovario fructificado poco más largo que ancho *A. asplundii* Thell. subsp. *australis* (Hunz.) N. Bayón

I. 1a. *Amaranthus asplundii* Thell. subsp. *asplundii*.

Amaranthus buchtienianus Thell., Repert. Spec. Nov. Regni Veg. 21: 323. 1925. TIPO: Bolivia. La Paz: Prov. Murillo, Sopocachi, 27 abr. 1921, *E. Asplund 3838* (lectotipo, designado por Bayón [2011: 174], S-R-254!; isoelectotipo, Z [código de barras] Z000000240!).

Amaranthus affinis Thell., Repert. Spec. Nov. Regni. Veg. 21: 324. 1925. TIPO: Bolivia. Cochabamba: Prov. Capinota, Capinota, ca. 2400 m, 11 jun. 1921, *E. Asplund 4147* (holotipo, S-R-251 no visto, imagen!).

Amaranthus asplundii subsp. *asplundii* se distingue porque en las flores con tres sépalos, el sépalo de mayor tamaño es angosto, igualando en longitud al ovario, el cual es apenas más largo que ancho.

Nombre vulgar. Ataco (*Cabrera 12153*, LP).

Ejemplares examinados. ARGENTINA. **Jujuy:** Dep. Humahuaca, Chuculesna, a 18 km de Humahuaca, *A. T. Hunziker 2074* (CORD); Caleta, *H. A. Fabris & J. V. Crisci 6843* (LP); Ruta Prov. 14, Qda. La Soledad, a 12 km de Humahuaca, *K. Okada 3043.1* (LP). Dep. Santa Catalina. Co. Santa Catalina, *P. Arenas & A. Dell'Arciprete 1746* (CTES). Dep. Tilcara, Huacalera, Qda. Abra de la Cruz, *A. L. Cabrera 12153* (LP). Dep. Tumbaya, Volcán, Chiclayo, *A. L. Cabrera et al. 16897* (LP). **Salta:** Dep. Rosario de Lerma, Incamayo Km. 56, *G. E. Barboza et al. 1465, 1466* (CORD). BOLIVIA. **La Paz:** Prov. Murillo, Sopocachi, 27 abr. 1921, *E. Asplund 2988* (paratipo, *Amaranthus buchtienianus*, S).

I. 1b. *Amaranthus asplundii* Thell. subsp. *australis* (Hunz.) N. Bayón, stat. nov. Basónimo: *Amaranthus asplundii* Thell. var. *australis* Hunz., Kurtziana 3: 207. 1966. TIPO: Argentina. Salta: Dep. Guachipas, Pampa Grande, 1600 m, 29 abr. 1942, *A. T. Hunziker 1759* (holotipo, CORD [código de barras] CORD00002455!).

Amaranthus asplundii subsp. *australis* se distingue porque en las flores con tres sépalos el sépalo mayor

es angosto, provisto de un breve mucrón; ovario claramente más largo que ancho.

Ejemplares examinados. ARGENTINA. **Salta:** Dep. Guachipas, Pampa Grande, 29 abr. 1942, A. T. Hunziker 1780 (paratipo, *Amaranthus asplundii* subsp. *australis*, CORD). Dep. La Viña, Qda. del Churqui, entre La Viña y Amblayo, 16 mar. 1943, A. T. Hunziker 2564, 2567, 2574, 2604 (paratipos, *A. asplundii* subsp. *australis*, CORD). BOLIVIA. **La Paz:** Prov. El Alto, B. Ruthsatz 722 (CTES).

I. 2. *Amaranthus cardenasianus* Hunz., Bol. Soc. Argent. Bot. 4 (1-2): 136. 1951. TIPO: Argentina. Salta: Dep. Guachipas, entre Cafayate y Alemania, ca. 1700 m, 24 mar. 1943, A. T. Hunziker 2807 (holotipo, CORD [código de barras] CORD00002457!; isotipo, MA-771390 no visto, imagen!). Figura 5.

Hierba anual; tallos principales erectos, 0.70–1 m, ramificado desde la base, glabros o subglabros. Hojas con pecíolo de 2–3.5 cm, glabras o glabrescentes, lámina ovado-rómbica, no ondulada, 4–8 × 2.5–4.5 cm, atenuada a cuneada en la base, haciéndose gradualmente más angosta hacia el ápice, éste agudo o subagudo, mucrón 1 mm. Inflorescencias terminales y axilares, las primeras en panojas, 12 × 3 cm, laxas, usualmente erectas, castaño claro; las segundas en glomérulos, escasos y menores; brácteas y bractéolas ovadas u oblongas, naviculares, 1–2 mm, menores que los sépalos, brevemente aristada o con mucrón 0.1–0.2 mm. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con 5 sépalos oblongo-lanceolados, 1.6–1.7 mm, obtusos, 5 estambres. Flores pistiladas urceoladas, con 5 sépalos espatulados, semejantes entre sí, 2.1–2.5 mm, reflejos, con la lámina expandida, redondeada o emarginada en el ápice, 1.3–1.8 mm de ancho, vena media de color verdoso, con 2–3 venas secundarias, sépalos apenas coalescentes en la base, adelgazados en el tercio inferior en una uña, 0.2–0.3 mm de ancho, lo que permite que se vea el ovario entre ellas; cáliz expandido en flores plenamente desarrolladas de 3.5–4 mm diám distalmente; estigmas tres, 0.2–0.3 mm, delgados. Frutos dehiscentes, más cortos que los sépalos, opérculo rugoso; semillas de color castaño-rojizo o negruzco, 1–1.1 mm, muy brillantes y lisas en el área central, apenas punteadas en el área marginal.

Distribución y ecología. Esta especie se distribuye en zonas montañosas del noroeste de Argentina, Bolivia y Perú, entre los 1200 m y los 3100 m, donde prefiere suelos secos y pedregosos (Cárdenas 4137, US; Llatas et al. 9126, MO). Florece y fructifica en los meses de enero y febrero (junio).

Discusión. *Amaranthus cardenasianus* se asemeja a *A. standleyanus*, *A. squamulatus* (americanas) y *A. undulatus* (australiana) por los sépalos de las flores pistiladas en número de cinco y de forma espatulada, y por las inflorescencias apicales (aunque no siempre presentes en *A. standleyanus* y *A. squamulatus*). De las dos primeras se puede distinguir porque *A. cardenasianus* tiene inflorescencias apicales más laxas y más anchas (3 cm contra 1–1.5 cm de ancho) y frutos dehiscentes (raro en *A. squamulatus*). Además, por un lado *A. standleyanus* presenta sépalos mucronados y por el otro, *A. squamulatus* tiene brácteas y bractéolas florales acuminadas terminadas en una arista erecta y rígida, mientras que *A. cardenasianus* carece de mucrón en sus sépalos y sus brácteas son brevemente aristadas o mucronadas. *Amaranthus undulatus* tiene inflorescencias terminales de 1 cm de ancho y los sépalos de sus flores pistiladas cuentan con un fuerte mucrón (o arista) de 0.5 mm, caracteres que no se corresponden con los de *A. cardenasianus*.

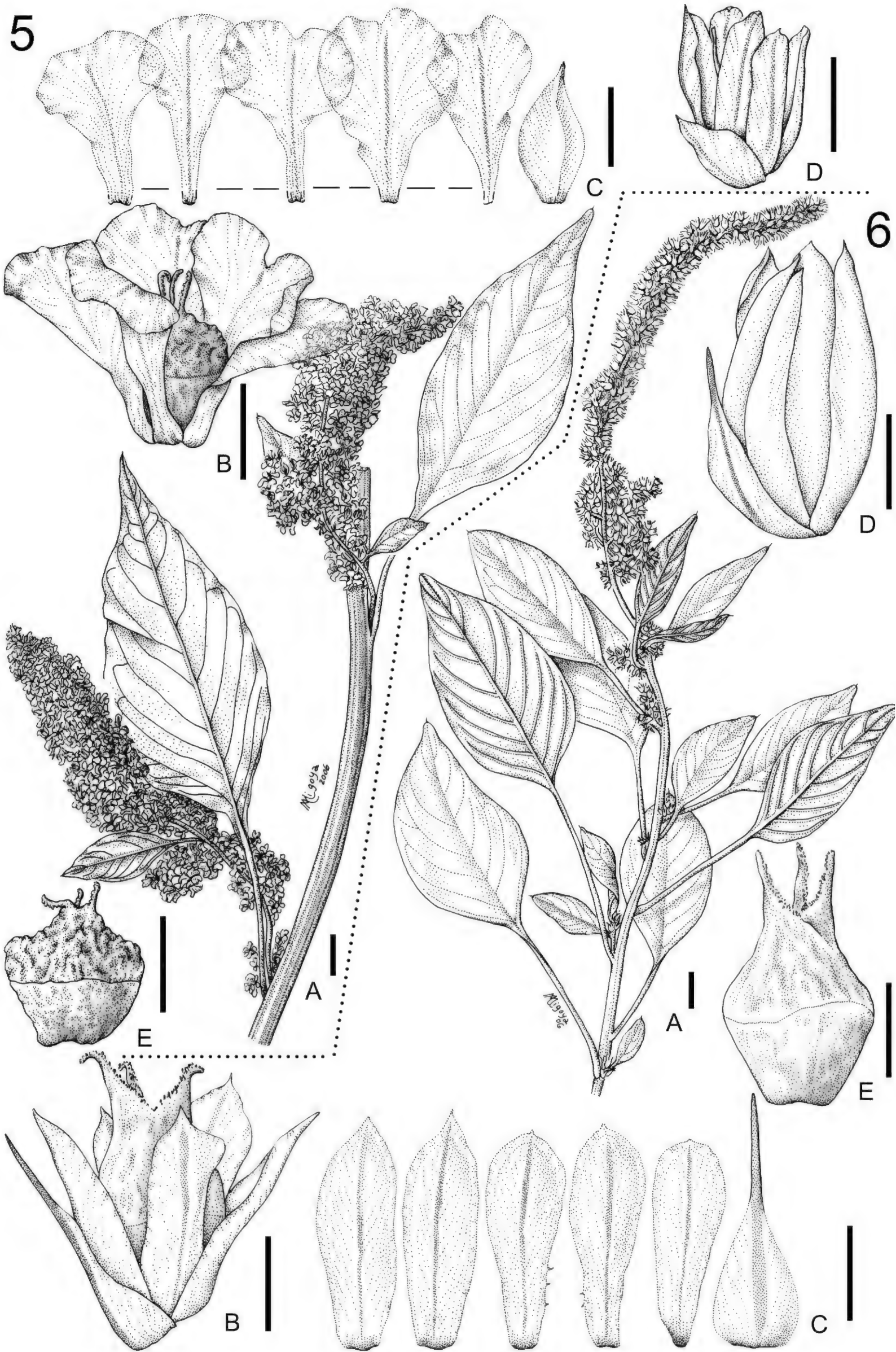
Ejemplares examinados. ARGENTINA. **Salta:** ca. Cachi, ene. 1897, C. L. Spegazzini s.n. (LP). BOLIVIA. **Chuquisaca:** Km. 30, bajada de Sucre a Chaquí Mayu, feb. 1949, M. Cárdenas 4137 (paratipo, *A. cardenasianus*, CORD, US). **La Paz:** Prov. Murillo, Calacoto, 30 km bajando el Río La Paz, G. Beck 7988 (CTES, MO). PERÚ. **Piura:** Huancabamba, Perculla, S. Llatas Quiros et al. 9126 (MO).

I. 3. *Amaranthus caudatus* L., Sp. Pl. 990. 1753. TIPO: “Habitat in Peru, Persia, Ceilán”, *Herb. Linnaeus 1117.26* (lectotipo, designado por Townsend [1974a: 10], LINN 1117.26 no visto, imagen!). Figura 6.

Amaranthus caudatus L. var. *alopecurus* Moq. in de Candolle, Prodr. 13(2): 256. 1849. TIPO: Etiopía. Adoam, 1 nov. 1844, G. W. Schimper 1535 (lectotipo, aquí designado, P [código de barras] P00482809 no visto, imagen!; isoelectotipos, GH [cb] GH00037040!, BR-835755 no visto, imagen!, HOH [cb] HOH009263 no visto, imagen!, K [cb] K000243569 no visto, imagen!, MO-37783 no visto, imagen!).

Figura 5. *Amaranthus cardenasianus* Hunz. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A–E, ilustrado de Cárdenas 4137 (US). La barra de escala para A = 1 cm; para B–E = 1 mm.

Figura 6. *Amaranthus caudatus* L. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A, ilustrado de Schimper 1535 (GH); B–E, de Burkart 17809 (SI). La barra de escala para A = 1 cm; para B–E = 1 mm.



Amaranthus mantegazzianus Passer., Ind. Sem. Hort. Bot. Parma 4. 1865. TIPO: Argentina. Tucumán: Dep. Tafí, Colalao del Valle, 23 mar. 1943, ca. 1700 m, A. T. Hunziker 2555 (neotipo, CORD [código de barras] CORD00002607!, designado por Hunziker [1951: 105]; isoneotipos, K [cb] K000582941 no visto, imagen!, SI-47100!, US-2269844 no visto, imagen!).

Amaranthus edulis Speg., Physis (Buenos Aires) 3: 163. 1917. TIPO: cultivado en La Plata, s.f., C. L. Spegazzini s.n. (holotipo, LPS-12665 en LP-16325!).

Hierba anual; tallos principales robustos, a veces arqueados, 1–1.5(–2) m, con pocas o muchas ramificaciones, pubescentes en la porción superior de la planta, cerca de la inflorescencia. Hojas con pecíolo de hasta 8 cm, pubescentes sólo sobre la vena media y principales venas secundarias en la cara abaxial, lámina rómbico-ovada a elíptica, no ondulada, de hasta 11 × 6 cm, atenuada a cuneada en la base, haciéndose más angosta gradualmente hacia el ápice, el cual puede ser obtuso o subagudo. Inflorescencias terminales y axilares, las primeras en panojas o espigas, de hasta 30(–40) × 4 cm, caudadas, vistosas, robustas, péndulas o erectas, por lo general de color rojo o púrpura, rara vez blancuzco o amarillo; las axilares del mismo aspecto, aunque menores, sólo en las hojas superiores; brácteas y bractéolas deltoides, 3–4 mm, iguales o hasta de 1.5 veces la longitud de los sépalos, espinescentes, ápice con arista 0.5–1.2 mm. Flores de ambos sexos sobre la misma inflorescencia. Flores estaminadas con 5 sépalos ovado-acuminados, 2–3.5 mm, 5 estambres. Flores pistiladas con 5 sépalos oblongo-obovados a espatulados, 1.5–2.5 mm, el o los internos obtusos o emarginados, de similar tamaño, solapados unos con otros, erectos o reflejos, con la vena media marcada, a menudo con mucrón 0.1–0.2(–0.5) mm; estigmas tres, 0.5–0.75 mm, divergentes o reflejos, más raro erectos. Frutos dehiscentes, con el opérculo arrugado o liso, más largos que los sépalos, adelgazándose gradual o abruptamente; semillas de color blanco-amarillento a castaño oscuro, 1–1.3 mm.

Distribución y ecología. *Amaranthus caudatus* es un pseudocereal originario de las zonas cordilleranas de América del Sur. Cultivada a los costados de cultivos de maíz (Cárdenas 3626, SI) en el Noroeste de Argentina (Bayón, obs. pers.), Bolivia, Ecuador y Perú (Bayón, obs. pers.). Cultivada en África, Asia, Australia y Europa. En este último continente empleada como ornamental (Hunziker, 1943; Sauer, 1950, 1967). Florece entre los meses de noviembre y abril (junio).

Nombres vulgares. Ataco (*Philipi* s.n., SGO); coimi, crista di galo (*Ferreya* 169, CTES); chaclión, chaquillón, chasquillón, coimi, kiwicha (*Krapovikas*

& Cristóbal 46661, 46662, 46663, CTES; Hunziker 2555, CORD, K); Inca pachaqui (Macbride, 1937); quinoa, quinoa blanca (Sauer, 1967); quinoa de Castilla, quinoa del valle, quinoa rosada, quinua, trigo inca (*Spegazzini* s.n., LP) (Hunziker, 1943, 1951b; de la Peña & Pensiero, 2004); love-lies-bleeding, purple amaranth, foxtail amaranth, quilete (Mosyakin & Robertson, 2003).

Discusión. *Amaranthus caudatus* es una especie cercana a *A. hybridus* subsp. *quitensis*, considerada su progenitora, y a las otras dos especies cultivadas: *A. cruentus* y *A. hypochondriacus*. De la primera se puede distinguir porque *A. caudatus* (rara vez escapada de cultivo) muestra inflorescencias muy grandes (mayores de 30 cm), caudadas, de colores vivos y con semillas frecuentemente de colores claros, caracteres que no se presentan en *A. hybridus*. De las otras dos formas cultivadas se diferencia dado que *A. hypochondriacus* tiene inflorescencias también grandes pero erectas y rígidas, y no flácidas y caudadas. Por otro lado, de *A. cruentus* se distingue pues los sépalos de esta última son agudos en el ápice (no como los internos de *A. caudatus* que son obtusos o emarginados), sus inflorescencias no son caudadas y los frutos forman un rostro al adelgazarse en forma abrupta (no en forma gradual como en *A. caudatus*).

Moquin (1849: 256) hace una breve diagnosis y menciona dos sintipos en el protólogo de *Amaranthus caudatus* var. *alopecurus*: “In Abyssiniae ruderalis prope Adoam, Schimper 1535 et 1077”. Del segundo de ellos he estudiado imágenes de los herbarios K, MO y S. Del primero, se han localizado seis isosintipos, de los que ha sido posible estudiar el depositado en el herbario GH, como así también las imágenes de sus duplicados existentes en BR, K [2], MO y P. El ejemplar de este último herbario (P [código de barras] P00482809), posee una rama con hojas e inflorescencias muy bien desarrolladas, correspondiéndose con los caracteres de la variedad descrita por Moquin en lo referido a las inflorescencias muy densas y ramosas, proponiéndoselo aquí como lectotipo de la variedad.

Ejemplares examinados. ARGENTINA. **Buenos Aires:** La Plata, cultivada, origen de la semilla Cafayate, Salta, A. Burkart 17809 (SI); La Plata, cult. de semilla proveniente de La Poma, Salta, C. L. Spegazzini s.n. (BAB); Castelar, cult. en el Jardín Botánico de Castelar, A. García s.n. (BAB-80817); cult. en Buenos Aires, semillas provenientes de Salta, abr. 1922, s. coll. (BA-32227). **Corrientes:** Cult., de material proveniente de Jujuy, A. Krapovickas 44414 (CTES). **Jujuy:** Dep. Tumbaya, cult. en huerta 2 km al N de Tumbaya, A. Krapovickas & C. Cristóbal 46661, 46662, 46663 (los tres en CTES). **Mendoza:** Chacras de Coria, culti. en la Facultad de Ciencias Agrarias, F. A. Roig 7356 (CTES). BOLIVIA. **La Paz:** Irupana, M. Cárdenas 3626,

3627 (ambos en SI). BRASIL. **Paraná:** Mpio. Curitiba, Barigui, *L. F. Ferreira* 169 (CTES). Mpio. Curitiba, Alto da XV, *R. Kummrow* 1368 (CTES). CHILE. Santiago y Antofagasta alta, abr. 1882 y ene. 1885, *F. Philippi* s.n. (SGO-038843).

ETIOPÍA. Adoam, *G. W. Schimper* 1077 (sintipo, *Amaranthus caudatus* var. *alopecurus* (K, MO, S).

I. 4. *Amaranthus cruentus* L., Syst. Nat., ed. 10, 2: 1269. 1759. TIPO: “China”, *Herb. Linnaeus* 1117.25 (lectotipo, designado por Townsend [1974a: 12], LINN 1117.25 no visto, imagen!). Figura 7.

Amaranthus flavus L., Syst. Nat., ed. 10, 2: 1269. 1759. TIPO: [India] “Habitat in India”, *Herb. Linnaeus* 1117.23 (lectotipo, designado por Iamónico [2014a: 147], LINN 1117.23 no visto, imagen!).

Amaranthus paniculatus L., Sp. Pl. ed. 2, 2: 1406. 1763. *Amaranthus hybridus* L. [sin rango] *paniculatus* (L.) Thell., Syn. Mitteleur. Fl. 5 (Abth. 1): 247. 1919, como “proles *paniculatus*”. *Amaranthus hybridus* L. subsp. *paniculatus* (L.) Heijny, Dostal, Kvetena CSR: 444. 1950. TIPO: Estados Unidos de América. “Habitat in America”, *Herb. Linnaeus* 1117.20 (lectotipo, designado por El Hadidi & El Hadidi [1981: 37], LINN 1117.20 no visto, imagen!).

Amaranthus sanguineus L., Sp. Pl. ed. 2, 2: 1407. 1763. *Amaranthus paniculatus* var. *sanguineus* (L.) Moq. in de Candolle, Prodr. 13(2): 257. 1849. *Amaranthus hybridus* var. *sanguineus* (L.) Farw. Rep. (Annual) Michigan Acad. Sci. 20: 175. 1918. TIPO: Reino Unido de Gran Bretaña. “Habitat in Bahama”, *Herb. Linnaeus* 1117.21 (lectotipo, designado por Iamónico [2014a: 148], LINN 1117.21 no visto, imagen!).

Hierba anual; tallos principales erectos, 0.5–1.5 m, poco o bastante ramificados, poco pubescentes cerca y en la inflorescencia, con pelos simples uniseriados. Hojas con pecíolo de hasta 5 cm, glabras o con algunos pelos sobre las venas principales sobre la cara abaxial, lámina rómbica, ovada u ovado-lanceolada, no ondulada, de hasta 12 × 6 cm, atenuada en la base, angostándose gradualmente hacia el ápice. Inflorescencias terminales, en panoja, grandes, con ramas algo curvadas, de hasta 30 × 10 cm, usualmente de color rojo; brácteas y bractéolas lanceoladas a angostamente espatuladas, 2–3 mm, iguales o apenas más largas que los sépalos, espinescentes, ápice con arista de 0.75–1 mm. Flores de ambos sexos sobre la misma inflorescencia. Flores estaminadas con 5 sépalos ovado-acuminados, 2–2.5 mm, 5 estambres. Flores pistiladas con 5 sépalos oblongo-lanceolados, 1.5–2.5 mm, agudos, acuminados, casi iguales entre sí (a veces el externo es 0.5 mm más largo que el resto y el interno puede no ser acuminado), rectos, con la vena media marcada; estigmas tres, 0.4–1 mm, erectos o apenas reflejos. Frutos dehiscentes, 2–2.5 mm, con el pericarpio liso o apenas arrugado sobre la línea de dehiscencia, adelgazándose en forma un tanto abrupta y dando

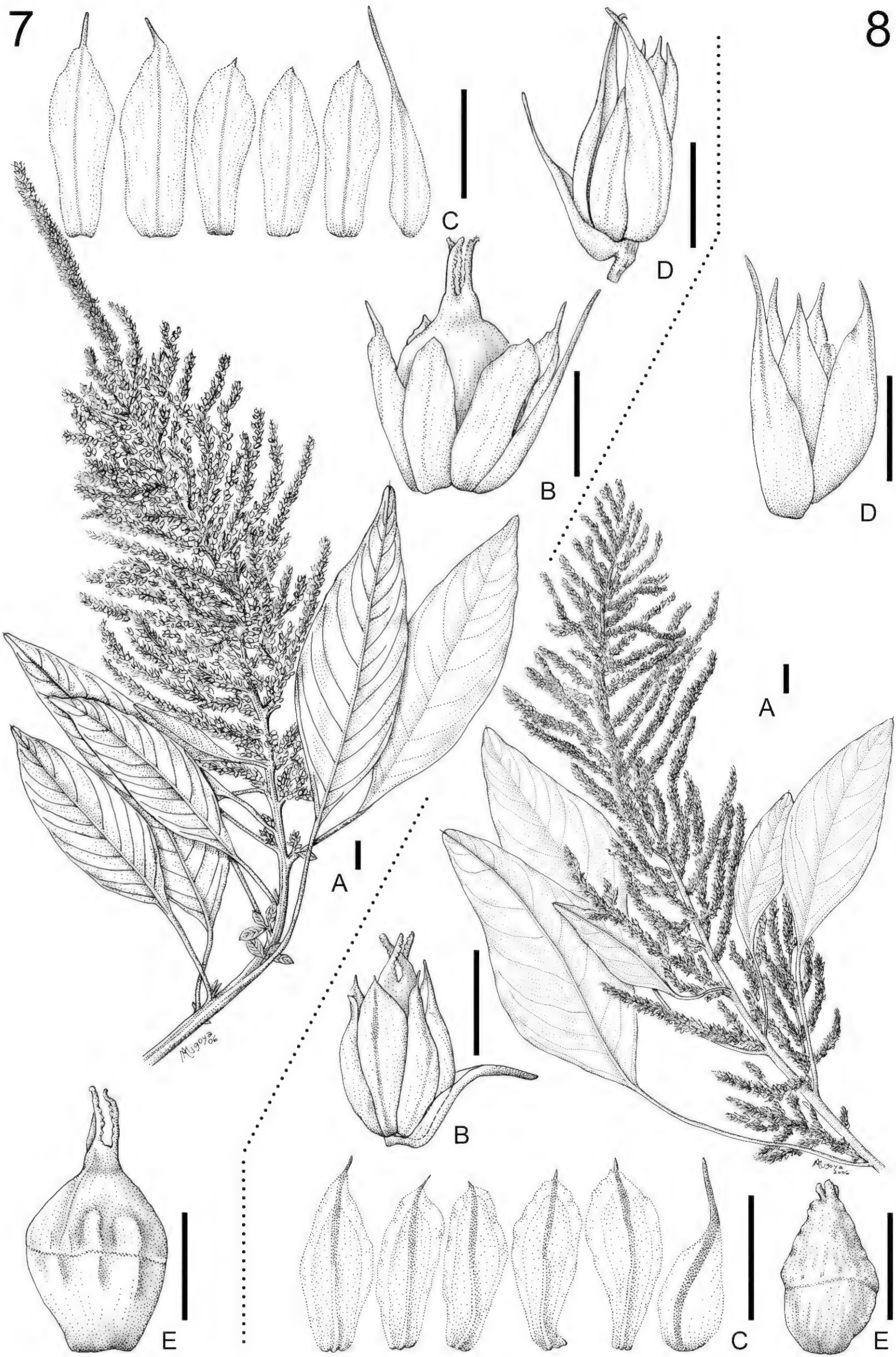
origen a un rostro corto y liso hacia la zona estigmática, a veces imperceptible, poco más largos que los sépalos; semillas de color blancuzco o amarillento, raramente castaño oscuro, 1.25–1.6 × 1.1–1.2 mm.

Distribución y ecología. *Amaranthus cruentus* es originaria de América Central (Guatemala y sur de México) y cultivada en el Nuevo y Viejo Mundo como pseudocereal, planta ornamental u hortaliza de hoja. Común en los patios de las viviendas (Bayón, obs. pers.; Keller & Gatti 1825, CTES). Su uso como pseudocereal está siendo revalorizado, conjuntamente con el de las especies *A. caudatus* y *A. hypocondriacus* (Sauer, 1950, 1967; Mosyakin & Robertson, 2003). Costea et al. (2001a) y Lanoue et al. (1996) la citan como hortaliza para África y para el este de Asia (Costea et al., 2003). Se suelen encontrar ejemplares escapados de cultivo. Florece entre los meses de enero y abril.

Nombres vulgares. Bledo (Sauer, 1967); ataco, bledo colorado, sangorache (Macbride, 1937); karuru (Keller & Gatti 1825, CTES); blood amaranth, purple amaranth, caterpillar amaranth (Mosyakin & Robertson, 2003).

Discusión. *Amaranthus cruentus* es semejante a *A. hybridus* subsp. *hybridus*, supuestamente su progenitora, y a otras dos especies cultivadas: *A. caudatus* y *A. hypocondriacus*. De la primera se distingue por ser una planta que crece bajo cultivo (*A. hybridus* subsp. *hybridus* es espontánea), por sus inflorescencias mayores de 30 cm, coloreadas al igual que las plantas. De *A. hypocondriacus* se la puede diferenciar por sus inflorescencias variables en aspecto, flácidas, péndulas o erectas (en *A. hypocondriacus* son siempre rígidas y erectas), por el rostro que se forma en la parte superior de su pericarpio (no adelgazándose gradualmente) y por sus brácteas y bractéolas florales de 2–3 mm (no de 3–6 mm). Por otro lado, de *A. caudatus* se distingue pues esta última presenta inflorescencias caudadas y sépalos internos obtusos o emarginados, mientras que *A. cruentus* no presenta inflorescencias caudadas y los sépalos son agudos.

Ejemplares examinados. ARGENTINA. **Buenos Aires:** Pdo. La Plata, cultivada, *N. D. Bayón* 627 (LPAG); La Plata, *N. D. Bayón* 608 (LPAG). Pdo. San Isidro, cult., *A. Burkart* 15577 (SI). **La Rioja:** Dep. Chilecito, Chilecito, Barrio Los Sarmientos, *N. D. Bayón* 1354 (LPAG). **Misiones:** Dep. Eldorado, Ruta Prov. 17, aldea aborigen Pozo Azul, *H. Keller & F. Gatti* 1825 (CTES). **Salta:** Dep. Cafayate, Cafayate, *A. Krapovickas & C. L. Cristóbal* 20559 (CTES). BOLIVIA. **La Paz:** Prov. Nor Yungas, Coroico, ca. Beljardín, *R. Zeballos* 1 (CTES). **Santa Cruz:** Velazco, *A. Krapovickas & A. Schinini* 32443 (CTES). COLOMBIA.



Nueva Granada, *J. Triana 961* (K). ECUADOR. **Cotopaxi:** around Pilalo, *L. Holm-Nielsen & S. Jeppesen 1520* (CTES).

SUDÁFRICA. **Transvaal:** White River, *L. Killian 10* (K).

GUATEMALA. **Alta Verapaz:** Santa Cruz Verapaz, Cubilquitz, *H. von Tuerckheim 8567* (K).

ESPAÑA. **Cataluña:** Gerona, jardines en Figueras, *F. Augustin 4094* (SI).

I. 5. *Amaranthus dubius* Mart. ex Thell., Fl. Adv. Montpell.: 203. 1912. TIPO: [país desconocido]. Material cultivado del Jardín Botánico de Erlangen, ex herb. Schwoegrichen (neotipo, designado por Townsend [1974b: 471], M [código de barras] M0107382 no visto, imagen!). Figura 8.

Amaranthus dubius Thell. var. *crassesplicatus* Suess., Mitt. Bot. Staats. München 1: 73. 1951. TIPO: Tanzania. Región Mbeya: Chunya Distr., Mlupa [Lupa], 30 oct. 1932, *Geilingeer 3011* (lectotipo, designado por Townsend [1985: 28], K [código de barras] K000190113 no visto, imagen!).

Amaranthus hybridus L. f. *acicularis* Suess., Mitt. Bot. Staats. München 1: 4. 1950. TIPO: Uganda. Masaka: Kabula, sep. 1945, *J. W. Purseglove 1813* (holotipo, K [código de barras] K000190112 no visto, imagen!).

Hierba anual; tallos principales usualmente erectos, de 0.3(–1.5) m, delgados a gruesos, simples o ramificados, glabros o corta e inconspicuamente pubescentes cerca de la inflorescencia. Hojas con pecíolo de hasta 8.5 cm, glabras o glabrescentes, lámina ovada o rómbico-ovada, no ondulada, 1.5–8(–12) × 0.7–5(–8) cm, ampliamente cuneada en la base, obtusa o retusa en el ápice, mucronada. Inflorescencias terminales y axilares, las primeras en una espiga simple, raramente ramificada, 3–15(–20) × 0.6–0.8(–1) cm, las segundas en glomérulos de 4–10 mm diám, todas ellas de color verdoso; brácteas y bractéolas ovado-deltoides, 1.3–1.7 mm, más cortas que los sépalos o casi igualándolos, mucronadas. Flores de los glomérulos inferiores enteramente pistiladas, mientras que las espigas terminales muestran en su ápice, a lo largo de ca. 1 cm (o menos) flores estaminadas (también ocasionalmente algunas flores estaminadas pueden estar esparcidas entre las pistiladas). Flores estaminadas con (4)5 sépalos lanceolados, ovados u oblongo-elípticos, por lo general acuminados, con la vena media de color verde, estambres 5. Flores pistiladas con (4)5 sépalos angostos, oblongos o elípticos, 1.5–2.7 mm, agudos con un breve acumen

u obtusos, el sépalo externo mayor que los restantes; estigmas tres, 0.75–1 mm, flexuosos y reflejos. Frutos dehiscentes, lisos o rugosos, con un rostro breve e inflado, casi tan largo como los sépalos o más breve; semillas de color negruzco a castaño-rojizo oscuro, 1–1.25 mm, apenas reticuladas.

Distribución y ecología. *Amaranthus dubius* es una especie de regiones tropicales, probablemente originaria de América, desde México y las Indias Occidentales hasta el norte de Perú y Brasil, pero hoy hallada prácticamente en los trópicos de todo el globo (Eliasson, 1987). Es más rara como adventicia en regiones templadas, principalmente de tierras bajas. A veces considerada maleza de montes frutales (*Parodi 8084*, LP; *Parodi 8536*, K), común en lugares donde se arrojan desperdicios cerca de las poblaciones o al costado de los caminos, o en pastizales donde es consumida por el ganado vacuno (*Llatas Quiroz 2264*, 2265, CTES), crece hasta los 300 m de altitud. En la Argentina florece y fructifica en los meses de marzo y abril.

Nombres vulgares. Yuyo hembra (*Llatas Quiroz 2264*, 2265, CTES); spleen amaranth (Mosyakin & Robertson, 2003).

Usos. *Amaranthus dubius* es estimada en Sri Lanka como hortaliza, como también en regiones cálidas y húmedas de África (Lanoue et al., 1996). Sus semillas se emplean como alimento para aves.

Discusión. *Amaranthus dubius* es una especie cercana a *A. spinosus*, *A. hybridus* y *A. tamaulipensis*. De *A. spinosus* es posible diferenciarla de forma inequívoca por la carencia de espinas, aunque otro carácter útil es el menor tramo (a lo sumo 1 cm) con flores estaminadas que *A. dubius* presenta en el ápice de sus inflorescencias terminales, siendo que en *A. spinosus* al menos la mitad de la inflorescencia apical tiene flores estaminadas, lo que representa más de 1 cm. De *A. hybridus* se puede distinguir porque esta especie tiene flores estaminadas entremezcladas con las pistiladas en todas sus inflorescencias, y por el mayor tamaño de sus brácteas y bractéolas florales, siendo en *A. dubius* generalmente menores que los sépalos de sus flores pistiladas y en *A. hybridus* generalmente mayores que éstos. *Amarantus tamaulipensis* cuenta con tres estambres, siendo cinco en *A. dubius*. Además, en *A. tamaulipensis* los sépalos de

Figura 7. *Amaranthus cruentus* L. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A–E, ilustrado de *Tuerckheim 8567* (K). La barra de escala para A = 1 cm; para B–E = 1 mm.

Figura 8. *Amaranthus dubius* Mart. ex Thell. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A–E, ilustrado de *Steyemark et al. 122886* (K). La barra de escala para A = 1 cm; para B–E = 1 mm.

las flores pistiladas carecen de márgenes membranáceos (son enteramente escariosos), son más breves que el fruto, están soldados en la base y bien separados entre sí, contrario a lo que se observa en *A. dubius*.

Amaranthus dubius es una especie interesante desde el punto de vista citológico, dado que es poliploide ($2n = 64$) (Grant, 1959). Según este autor sería un alotetraploide siendo *A. spinosus* uno de los progenitores y posiblemente *A. hybridus* (denominada *A. quitensis*) el otro. Townsend (1980) también afirma que esas dos especies serían los padres de *A. dubius*. De acuerdo a Townsend (1985) los híbridos entre *A. dubius* y *A. spinosus* aparecen libremente cuando estas dos entidades se asocian en África tropical. El rasgo que permite distinguir a estos taxones son las espinas, aunque el mayor número de flores estaminadas en las espigas de *A. spinosus* parece ser un carácter interesante cuando se coleccionan las inflorescencias terminales.

Ejemplares examinados. ARGENTINA. **Buenos Aires:** Pdo. Pergamino, J. A. Peña, *L. R. Parodi 8084*, 8536 (ambos en K). BOLIVIA. **Tarija:** Prov. O'Connor, Entre Ríos, *A. Krapovickas & A. Schinini 39073* (CTES). ECUADOR. **Galápagos:** Isla Santa Cruz (Chávez, Indefatigable), *T. W. J. Taylor 136* (K). PERÚ. **Chiclayo:** Dep. Lambayeque, Reque, *S. Llatas Quiroz 2264*, 2265 (ambos en CTES). VENEZUELA. **Distrito Federal:** Mpio. Vargas, Catia la Mar, *A. Castillo 2507*, 2552 (ambos en CTES). Mpio. Vargas, Catia la Mar, *N. Xena 1019* (CTES). **Zulia:** Distr. Mara, ca. Río Guasare, entre Rancho 505 y Co. Yolanda, *J. A. Steyermark et al. 122886* (K).

FRANCIA. **Haut Rhin:** *T. M. Pedersen 23* (CTES).

I. 6. *Amaranthus fimbriatus* (Torr.) Benth. ex S. Watson, Bot. California 2: 42. 1880. Basónimo: *Sarratia berlandieri* Moq. var. *fimbriata* Torr. in W. H. Emory, Bot. Mex. Bound. 2(1): 179. 1859. *Amblogyna fimbriata* (Torr.) A. Gray, Proc. Amer. Acad. 5: 168. 1861. TIPO: Estados Unidos de América. Texas: El Paso Co., Rio Grande Valley, ca. El Paso, 11 oct. 1849, *C. Wright 1294* (lectotipo, designado por Turner [2004: 9], GH [código de barras] GH00037158 no visto, imagen!). Figura 9.

Amaranthus venulosus S. Watson, Proc. Amer. Acad. 17: 376. 1882. TIPO: Estados Unidos de América. Arizona: Cochise Co., Apache Pass, 1881, *J. G.*

Lemmon 491 (lectotipo, designado por Turner [2004: 9], GH [código de barras] GH00037016 no visto, imagen!).

Sarratia berlandieri Moq. var. *denticulata* Torr., Rep. U. S. Mex. Bound., Bot. [Emory] 2(1): 179. 1859. *Amaranthus fimbriatus* (Torr.) S. Watson var. *denticulatus* (Torr.) Uline & W. L. Bray, Bot. Gaz. 19: 270. 1894. TIPO: México. Sonora: Santa Cruz, 25 sep. 1851, *G. Thurber s.n.* (holotipo, NY [código de barras] NY00991142 no visto, imagen!; isotipos, GH [cb] GH00037015 no visto, imagen!, NY [cb] NY01043130 no visto, imagen!).

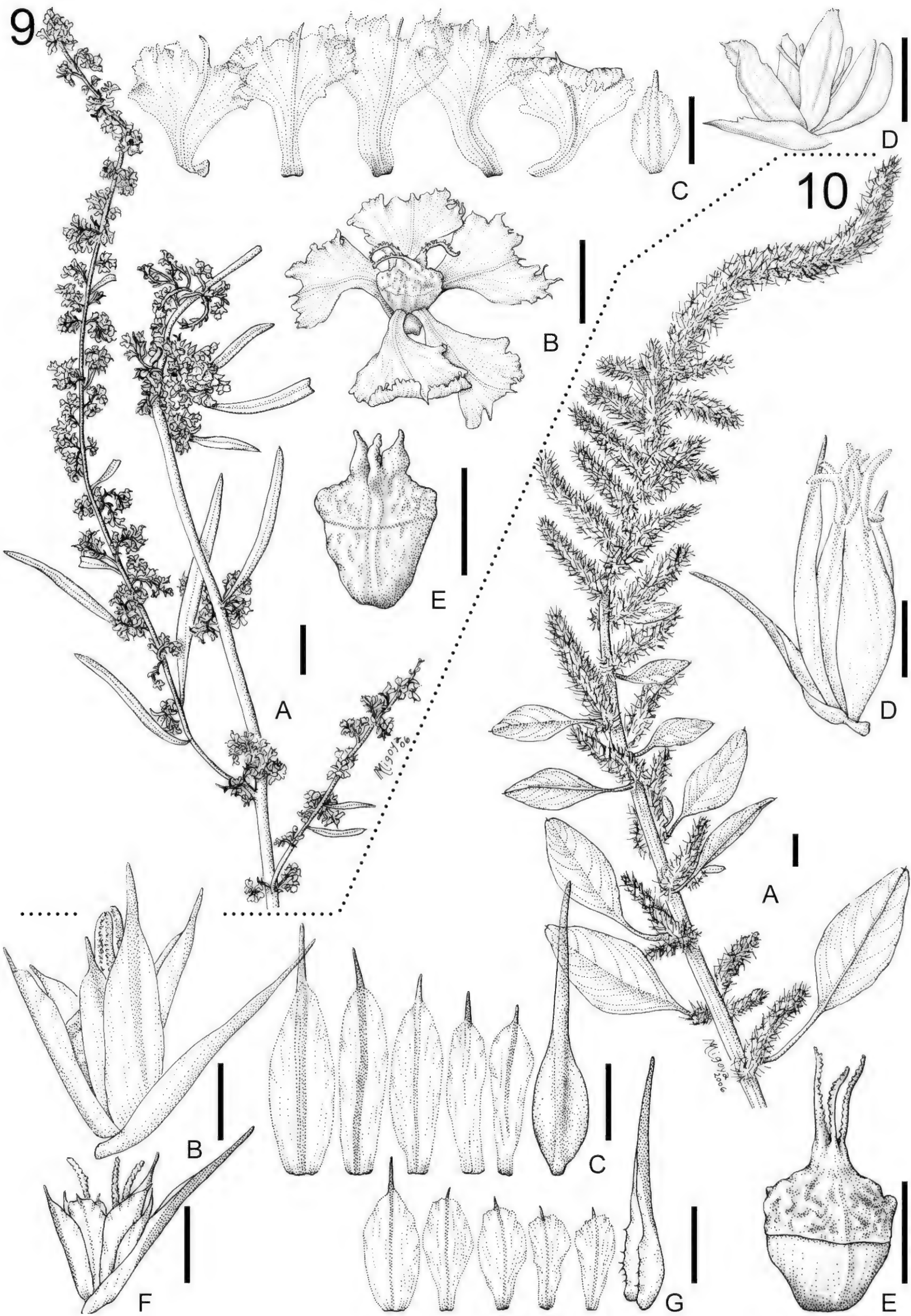
Hierba anual; tallos principales erectos o ascendentes, simples o con ramas laterales, que nacen desde la base, 0.3–0.7(–1) m, glabros. Hojas con pecíolo de 0.5–3 cm, glabras, lámina linear a linear-lanceolada, no ondulada, 2–6(–10) × 0.1–0.5(–2) cm, cuneada en la base, aguda en el ápice, mucronada. Inflorescencias terminales y axilares, las primeras en espigas, delgadas a gruesas, interrumpidas o continuas, de hasta 30 × 1(–2) cm; las segundas en glomérulos de hasta 1 cm diám; brácteas y bractéolas ovadas, acuminadas, membranáceas, con la vena media marcada y excurrente, menores que los sépalos, 1–1.8 mm. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con 5 sépalos oblongos a lanceolados, 1.1–1.5 mm, ápice obtuso, sólo algunas veces agudo, mucronados, estambres (2)3. Flores pistiladas con 5 sépalos ampliamente espatulados o flabelados, 1.5–3.3 mm, márgenes denticulados a fimbriados, adelgazados en una uña en la base, esta apenas esponjosa, casi iguales; estigmas 3, de hasta 0.8 mm. Frutos dehiscentes, con el opérculo fuertemente rugoso, urna apenas rugosa a casi lisa, más cortos que los sépalos; semillas de color castaño oscuro, 1 × 0.7–0.8 mm, muy brillantes en el centro, punteadas y opacas en el margen.

Distribución y ecología. *Amaranthus fimbriatus* es conocida en el Norte de México y sudoeste de los Estados Unidos de América. Prefiere suelos gravosos de desiertos y también hábitats disturbados, entre 500 m y 1700 m (*Landrum 7736*, CTES; *Munz 13889*, LP) (Mosyakin & Robertson, 2003). Florece entre los meses de agosto y diciembre.

Nombre vulgar. Fringed amaranth (Mosyakin & Robertson, 2003).

Figura 9. *Amaranthus fimbriatus* (Torr.) S. Watson. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A–E, ilustrado de *Munz 13889* (LP). La barra de escala para A = 1 cm; para B–E = 1 mm.

Figura 10. *Amaranthus hybridus* L. subsp. *hybridus*. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. *Amaranthus hybridus* subsp. *quitensis* (Kunth) Costea & Carretero. —F. Flor pistilada. —G. Sépalos y bráctea de la flor pistilada. A–E, ilustrado de *Bayón 1097* (LPAG); F–G, de *Bayón 642* (LPAG). La barra de escala para A = 1 cm; para B–G = 1 mm.



Discusión. *Amaranthus fimbriatus* es muy cercana a *A. torreyi* y *A. obcordatus* por poseer hojas delgadas, lineares a lanceoladas, inflorescencias en espigas terminales, no (o casi no) ramificadas y sépalos de las flores pistiladas espatulados o flabelados, contraídos en una uña basal. *Amaranthus torreyi* presenta los bordes de los sépalos de las flores pistiladas enteros, no denticulados a fimbriados como en *A. fimbriatus*, mientras que *A. obcordatus* tiene frutos indehiscentes, no dehiscentes como *A. fimbriatus*.

Ejemplares examinados. MÉXICO. **Baja California:** extremo S de la Isla Espíritu Santo, *I. L. Wiggins 15598* (K). **Sonora:** Santa Cruz, 25 sep. 1851, *G. Thurber s.n.* (sintipo, *Amaranthus venulosus*, GH-00037014 no visto, imagen!); Guaymas, *E. Palmer 154* (K).

ESTADOS UNIDOS DE AMÉRICA. **Arizona:** Maricopa Co., South Mtns., Pima Canyon rd., *L. R. Landrum 7736* (CTES); Gran Cañón, Meseta del Colorado, abr. 1884, *Moseley s.n.* (K); Rucker Valley, 1881, *J. G. Lemmon 490* (sintipo, *A. venulosus*, GH-00037017 no visto, imagen!); Pima Co., Tucson, Tumamoc Hill, *D. K. Warren & R. M. Turner 68-207* (LIL). **California:** 2 mi. N de Goffs, al E del Condado de San Bernardino, *P. A. Munz 13889* (LP); Bahía de Los Ángeles, Golfo de California, *E. Palmer 515* (K); Riverside Co., 2.4 mi. O de Valerie, 23 nov. 1948, *W. I. & B. E. Follett s.n.* (LIL-316914).

I. 7. *Amaranthus hybridus* L., Sp. Pl. 990. 1753.
Galliardia hybrida (L.) Nieuwl., Amer. Midl. Naturalist 3: 274. 1914, comb. inval. [*Galliardia Bubani*, nom. nud.]. TIPO: Suecia. Cultivado en Uppsala, "Habitat in Virginia", *Herb. Linnaeus 1117.19* (lectotipo, designado por Townsend [1974a: 19], LINN 1117.19 no visto, imagen!). Figura 10.

Hierba anual; tallos principales usualmente erectos, algunas veces ascendentes, 0.15–2(–3) m, ramificados, glabros a escasamente pubescentes, sobre todo cerca de la inflorescencia, a menudo con tonalidades de color rojizo. Hojas con pecíolo de hasta 13 cm, glabras o glabrescentes, con algunos pelos sobre la vena media en la cara abaxial, lámina de forma variable, ampliamente lanceolada, rómbica u ovada, no ondulada, 3–15 × 1.5–7 cm, atenuada a cuneada en la base, adelgazándose gradualmente hacia el ápice, éste obtuso a subagudo, mucronado. Inflorescencias terminales y axilares, las primeras en panoja con abundantes ramificaciones, de hasta 30 × 10 cm, con el eje apical a veces curvado, usualmente laxa, con ramas flexibles que se separan del eje central; las axilares en espigas axilares generalmente simples o poco ramificadas; de color verde con tonalidades rojizas o purpúreas; brácteas y bractéolas lanceolado-deltoides a deltoide-ovadas, de 2–4 mm, superando apenas en longitud a los sépalos o incluso

duplicándolos, espinescentes, ápice acuminado, provisto de una arista larga. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con 5 sépalos ovados a oblongo-lanceolados, 1.5–3 mm, 5 estambres. Flores pistiladas con 5 sépalos lanceolados u oblongos, 1.5–3.5 mm, agudos, acuminados o aristados, o el interno subagudo o aun obtuso, en este caso desiguales entre sí; estigmas (dos)tres, 0.25–1.6 mm. Frutos dehiscentes, con el opérculo liso o surcado longitudinalmente, con un rostro moderadamente marcado; algunos ejemplares con frutos indehiscentes, considerados como una especie distinta bajo el nombre de *Amaranthus bouchonii* o como variantes subespecíficas; semillas de color castaño-negruzco, 0.75–1.25 mm diám, brillantes en el área central, algunas veces algo más pálidas y menos brillantes, con el área marginal finamente reticulada.

Discusión. *Amaranthus hybridus* (en sentido amplio) ha sido la progenitora de al menos dos de las especies cultivadas como pseudocereales: *A. caudatus* y *A. cruentus*. La diferencia con ellas, y con *A. hypochondriacus*, se halla primeramente en que *A. hybridus* presenta por lo general inflorescencias menores de 30 cm de longitud, de color verde o a lo sumo con tonalidades de color rojizo, pero generalmente no de color rojo, púrpura o amarillo, siendo sus semillas siempre oscuras. De *A. powellii* se puede distinguir porque esta especie tiene brácteas y bractéolas más largas (4 mm o mayores), con inflorescencias de ramas rígidas y erectas, mientras *A. hybridus* tiene brácteas de menos de 4 mm, con inflorescencias de ramas flácidas que tienden a separarse del raquis.

Brenan (1961, 1981) y Townsend (1974a, 1974b, 1985) consideran a *Amaranthus hybridus* en un sentido amplio, incluyendo dentro de *A. hybridus* subsp. *hybridus* a *A. hypochondriacus* y a *A. powellii*, y dentro de *A. hybridus* subsp. *cruentus* (Townsend, 1974a, 1974b, 1985) y *A. hybridus* subsp. *incurvatus* (Brenan, 1961, 1981) a *A. cruentus*.

Se trata de una especie sumamente variable sobre la que los distintos autores han mostrado criterios muy disímiles al momento de tratarla. Algunos han visto a *Amaranthus quitensis* Kunth como un sinónimo de *A. hybridus*, mientras que en el otro extremo se les ha otorgado rango específico a ambos taxones. Otros en cambio han considerado a *A. quitensis* como subespecie o como variedad de la segunda. Sauer (1950, 1967) considera a estas dos entidades como distintas especies, caracterizando a *A. quitensis* por sus sépalos externos oblongos o apenas obovados y agudos, y los internos obovados a anchamente espatulados y obtusos. Agrega que los sépalos son más largos que los frutos maduros y

definidamente recurvos. En cuanto a *A. hybridus* establece que los sépalos son aproximadamente del mismo largo que los frutos maduros, apenas recurvos, siendo los externos oblongos y agudos, y los internos obovados y agudos. La principal diferencia queda establecida entonces por la forma y el ápice de los sépalos internos. En los distintos tratamientos florísticos de América del Sur ha primado la inclusión de *A. hybridus*: en la Flora de Perú (Macbride, 1937) se menciona únicamente a *A. hybridus*, al igual que en la Flora Ilustrada Catarinense (Smith & Downs, 1972) y en la Flora de Ecuador (Eliasson, 1987). Sólo este último autor cita a *A. quitensis* como un sinónimo. Covas (1941) le da a *A. quitensis* el rango de variedad dentro de *A. hybridus*, basándose en que las flores femeninas tienen al menos dos sépalos espatulados, algo mayores que el fruto. Sin embargo, el mismo Covas (1984: 336) se rectifica expresando que “no se considera apropiado dar status de especie, ni aún de variedad, al taxón *quitensis*”. Contrariamente, Hunziker (1966) considera exclusivamente al nombre *A. quitensis*. En las distintas floras de la Argentina ha prevalecido el uso del nombre de *A. quitensis* (Fabris, 1967; Cabrera & Zardini, 1978; Pedersen, 1984, 1994), sin mencionar a *A. hybridus* como uno de sus sinónimos. Sólo Fabris (1967) plantea la coexistencia de ambos taxones, aunque duda de la presencia de *A. hybridus* para la provincia de Entre Ríos. Finalmente, Pedersen (1999) incluye a *A. quitensis* dentro de la flora argentina, excluyendo explícitamente a *A. hybridus*. Coons (1977) se aboca al estudio del problema de la validez de estos dos taxones realizando un detallado estudio morfológico. Centra su análisis en los caracteres florales de las flores pistiladas (empleados originalmente por Sauer), esto es: dimensiones de los sépalos externos e internos y de sus respectivas bractéolas. Basándose en dichos caracteres concluye que no es posible distinguir a estas dos entidades. Finalmente, Costea et al. (2001a) consideran al taxón *quitensis* con el rango de subespecie de *A. hybridus*. Expresan como argumentos a favor la proximidad entre ambos y a la vez la disimilitud. Sostienen que los híbridos entre *A. hybridus* subsp. *hybridus* y *A. hybridus* subsp. *quitensis* presentan una viabilidad del polen del 60% (Greizerstein & Poggio, 1992), que el cariotipo muestra ciertas diferencias (Greizerstein et al., 1997) y que existen evidencias moleculares que las diferencian (Chan & Sun, 1997). Agregan que los caracteres del polen también posibilitan una clara distinción. En el presente tratamiento se adopta el criterio de Costea et al. (2001a) expuesto en la siguiente clave dicotómica.

CLAVE PARA LA DIFERENCIACIÓN DE LAS SUBESPECIES DE
AMARANTHUS HYBRIDUS

1. Sépalos internos angostamente ovados a oblongo-lanceolados, agudos o subagudos, erectos, más breves que el fruto ... *A. hybridus* L. subsp. *hybridus*
- 1'. Sépalos internos espatulados a obovados, obtusos o truncados, casi erectos o reflejos, más largos (raramente iguales) al fruto *A. hybridus* L. subsp. *quitensis* (Kunth) Costea & Carretero

I. 7a. *Amaranthus hybridus* L. subsp. *hybridus*.

Amaranthus chlorostachys Willd., Hist. Amaranth. 34. 1790. *Amaranthus hybridus* L. var. *chlorostachys* (Willd.) Thell., Fl. Advent. Montpellier 205. 1912. TIPO: *Herb. Willdenow* (holotipo, B [código de barras] BW17521-010 no visto, imagen!).

Amaranthus patulus Bertol., Comment. Itin. Neapol. 19. 1837. *Galliaria patula* Bubani, Fl. Pyren. 1: 187. 1897, comb. inval. [*Galliaria* Bubani, nom. nud.] *Amaranthus hybridus* L. var. *patulus* Thell., Fl. Advent. Montpellier 8: 206. 1912. TIPO: Italia. Campania: Nápoles a Pasconcello, sep. 1834, *Bertoloni s.n.* (lectotipo, designado por Iamónico [2014b: 7], BOLO no visto, imagen!).

Amaranthus incurvatus Gren. & Godr., Fl. France Prosp. 8. 1846. *Amaranthus hybridus* L. subsp. *incurvatus* (Gren. & Godr.) Brenan, Watsonia 4: 268. 1961. TIPO: Francia. Lyon: Tigneu, 1845, *Timeroy s.n.* (holotipo, P [código de barras] P00502852 no visto, imagen!).

Amaranthus bouchonii Thell., Monde Pl. 27(160): 4. 1926. *Amaranthus hybridus* L. subsp. *bouchonii* (Thell.) O. Bolòs & Vigo, Butl. Inst. Catalana Hist. Nat., Secc. Bot. 38: 89. 1974. *Amaranthus hybridus* L. var. *bouchonii* (Thell.) Lambinon, Candollea 52: 273. 1997. *Amaranthus powellii* S. Watson subsp. *bouchonii* (Thell.) Costea & Carretero, Sida 19(4): 964. 2001. TIPO: Francia. Aquitaine: Bordeaux, 25 sep. 1925, *A. Bouchon s.n.* (lectotipo, designado por Iamónico [2014b: 2], US [código de barras] US00106237 no visto, imagen!; isoelectotipo, Z [cb] Z000000238!).

Amaranthus hybridus subsp. *hybridus* se caracteriza por tener los sépalos interiores angostamente ovados a oblongo-lanceolados, agudos o subagudos, erectos, más breves que el fruto.

Distribución y ecología. La subespecie autonómica de *Amaranthus hybridus* es nativa del este de América del Norte, México, América Central y América del Sur, creciendo entre los 700 m y los 3300 m (Brenan, 1981; Eliasson, 1987; Costea et al., 2001a; Mosyakin & Robertson, 2003; Palmer, 2009) y se encuentra como maleza de cultivos de maíz (*Boelcke & Gimara* 6, CTES). Mientras que en el hemisferio sur florece entre los meses de noviembre y mayo, en el hemisferio norte lo hace entre los meses de julio y septiembre.

Nombres vulgares. Ajara, aroma (*Hilgert & Lamas* 1678, CTES); green amaranth, green pigweed,

hybrid amaranth, smooth amaranth, smooth pigweed (Mosyakin & Robertson, 2003).

Usos. Se cultiva como ornamental y hortaliza (Hilgert & Lamas 1678, CTES).

Discusión. He tenido la oportunidad de estudiar el isoelectotipo de *Amaranthus bouchonii* que consiste en una porción de tallo con algunas pocas hojas y una inflorescencia apical poco desarrollada. De la observación de este ejemplar se desprende su similitud con *A. hybridus* subsp. *hybridus*, por sus sépalos oblongos y agudos y sus brácteas y bractéolas agudas, de ca. de 3 mm. Costea et al. (2001a) consideran que *A. bouchonii* es en verdad una subespecie de *A. powellii* y no de *A. hybridus*, aunque según el criterio aquí seguido para pertenecer a *A. powellii* debería mostrar brácteas y bractéolas de mayor longitud (4.5–6 mm), dos o tres veces más largas que los sépalos.

Ejemplares examinados. ARGENTINA. **Buenos Aires:** Pdo. La Plata, La Plata, *N. D. Bayón* 1097, 1540 (ambos en LPAG); Los Hornos, *N. D. Bayón* 629 (LPAG). **Catamarca:** Dep. Belén, Las Mansas, *R. Schreiter* 10471 (CTES); Hualfín, 10 mayo 1946, *P. V. de Droghetti* s.n. (CTES); Dep. Santa María, Fuerte Quemado, *M. Villafañe* 1275 (CTES); Santa María, *M. Villafañe* 1109 (CTES). **Córdoba:** Dep. Calamuchita, Sa. Grande, falda E: al pie del Co. Champaquí, *A. T. Hunziker* 9609, 9672 (ambos en CORD); Dep. Punilla, Sa. Grande, al pie del del Co. los Gigantes, *A. T. Hunziker* 8904 (CORD); Sa. Grande, falda E: Ea. San Bernardo, *A. T. Hunziker* 11980, 11981, 12004 (los tres en CORD); Dep. Totoral, Sa. Chica, Ea. San Miguel, *A. T. Hunziker* 4863, 4869 (ambos en CORD); Dep. Capital, estribación E de la Sa. de Velazco ca. de la mina El Cantadero, *A. T. Hunziker* 5243 (CORD); Dep. Punilla, Thea, *M. Villafañe* 615 (CORD). **Entre Ríos:** Salto Grande, *N. S. Troncoso et al.* 3572 (CTES). **Jujuy:** Dep. Humahuaca, Escuela Normal de Maestros, *O. Boelcke & J. Gimara* 6 (CTES). Dep. Tilcara, Tilcara, *H. A. Fabris* 6041 (LP); ca. Tilcara, *A. L. Cabrera et al.* 13372 (LP). Dep. Humahuaca, Ruta Prov. 14, Qda. de la Soledad, a 12 km de Humahuaca, *K. Okada* 3043.2 (LP). **Salta:** Dep. Rosario de Lerma, Campo Quijano, *D. Abbiatti & L. Claps* 1018 (LP). Dep. Orán, Lizarazu, *N. Hilgert & M. L. Lamas* 1678 (CTES). **San Juan:** Dep. Iglesia, Rodeo, *R. Kiesling & I. Peralta* 6998 (SI); Dep. Zonda, Ea. Maradona, Agua Pinto, *R. Kiesling et al.* 6019 (CTES). **BOLIVIA. La Paz:** ca. de La Paz, *M. Bang* 97 (K); Prov. Murillo, *G. Beck* 1396 (CTES). **CHILE. Región Metropolitana de Santiago:** Santiago, 1829, s. coll., s.n. (SGO-048382). **Arauco, VIII Región:** Bío-Bío, Contulmo, *T. M. Pedersen* 14108 (CTES). **Coquimbo, IV Región:** *Laturno* 1320 (SGO).

CHINA. Zhejiang: Xiangshan. Beijing, *B. M. Wang* 93 (BAB).

NAMIBIA. Rietfontein, *Janse* 297 (SI). **SUDÁFRICA. East Transvaal:** Pretoria, *K. A. Lansdell* 628 (BA).

AUSTRALIA. South Australia: Adelaide Plains, Marion Rd., *B. Copley* 1311 (SI). **NUEVA ZELANDA.** North Island, jun. 1909, *Travers* s.n. (SI-5585), mayo 1900, *Travers* s.n. (SI-5581).

ALEMANIA. Basel: Schutt bei Klein-Riehen, 11 sep. 1933, *Aellen* s.n. (BA, LP); Stuttgart, Stuttgart, 1866,

Spegazzini s.n. (LP). **AUSTRIA.** Styria, *T. M. Pedersen* 9789 (CTES). **ESPAÑA. Andalucía:** Almería, Cuevas de Vera, *F. Sennen & Jerónimo* 7261 (SI). **Cataluña:** Gerona, *F. Sennen* 7440 (SI). Barcelona, Manlleu, *Gonzalo* 4212, 5541, 6322 (los tres en SI); Manlleu, *F. Sennen* 4028, 4030 (ambos en SI); 12 oct. 1926, *Sennen* s.n. (SI); *F. Sennen* 5044, 6650 (ambos en SI). **FRANCIA. Córcega:** Solenzara, 18 jul. 1933, *P. Aellen* s.n. (LP). **Aquitaine:** Guyenne, Río Dronne, 21 ago. 1852, *A. Jordan* 187, *A. Jordan* s.n. (ambos en Z).

ESTADOS UNIDOS DE AMÉRICA. Maryland: Charlton Heights, 18 ago. 1894, *T. H. Kearney* s.n. (BAB). **Massachusetts:** Hampshire Co., *H. E. Ahles* 81287 (LP). **Texas:** *J. L. Berlandier* 2276 (NY).

I. 7b. *Amaranthus hybridus* L. subsp. *quitensis* (Kunth) Costea & Carretero, Sida 19(4): 955. 2001. Basónimo: *Amaranthus quitensis* Kunth, Nov. Gen. Sp. [H.B.K.] 2(folio): 156 [ed. cuarto 2: 194.] 1817. *Amaranthus quitensis* Kunth var. *stuckertianus* Thell., Syn. Mitteleur. Fl. 5 (abth. 1): 355. 1919. *Amaranthus hybridus* L. var. *quitensis* (Kunth) Covas, Darwiniana 5: 336. 1941. *Amaranthus retroflexus* L. subsp. *quitensis* (Kunth) O. Bolòs & Vigo, Butl. Inst. Catalana Hist. Nat., Secc. Bot. 38(1): 89. 1974. TIPO: Ecuador. “Crescit in ripa fluvii Guallabamba, alt. 1030 hex, (Regno Quitensi)”, jun. 1802, *Humboldt & Bonpland* 3082 (holotipo, P [código de barras] P00136030, no visto, imagen!).

Amaranthus artineanus Muschl., Man. Fl. Egypt. 1: 311. 1912, syn. nov. TIPO: Egipto. Chabral, 9 jul. 1887, *E. Sickenberger* s.n. (holotipo, Z [código de barras] Z000000235!; isotipo, Z [cb] Z000000236!).

Amaranthus hybridus subsp. *quitensis* se caracteriza por tener los sépalos interiores espatulados u obovados, obtusos o truncados, erectos o reflejos, por lo general más largos que el fruto.

Distribución y ecología. *Amaranthus hybridus* subsp. *quitensis* es originaria de las regiones tropicales y templado-cálidas de América del Sur. Se trata de una planta ruderal, que crece en las banquinas de los caminos y sobre los terraplenes de ferrocarril (*Fernández et al.* 88, CTES; *Cabrera* 6312, LP), siendo pionera en riveras de cursos de agua (*Cabrera* 7459, LP). Puede convertirse en maleza de importancia (*Scappini* 1705, CTES; *Quarín* 652, CTES) y crece entre el nivel del mar y los 3400 m (*Saravia Toledo* 15255, CTES) (Pedersen, 1987, 1994; Carrizo & Isasmendi, 1998). Esta subespecie prefiere lugares con temperaturas más elevadas que *A. hybridus* subsp. *hybridus*. Se ha encontrado como introducida ocasionalmente en Australia y en Europa continental, estando naturalizada en las islas Azores y Baleares. En la Argentina florece entre los meses de enero y mayo (junio, septiembre).

Nombres vulgares. Aroma (*Hilgert 1917*, CTES), ataco (*Brizuela 1150*, CTES); jataco, tataco (Macbride, 1937); bleado, caá-rurú, caá-rurú guazú, hierba colorada, moco de pavo, penacho, yuyo colorado (*Montes 1843*, LP; *Bordón s.n.*, CTES-410448) (Carrizo & Isasmendi, 1998; de la Peña & Pensiero, 2004).

Uso. Cultivada como ornamental (*Fonnegra et al. 2785*, CTES; *Hilgert 1917*, CTES).

Discusión. En la descripción original de *Amaranthus quitensis* Kunth (1817: 194) menciona al río Guallabamba en las cercanías de Quito, pero no especifica el número del ejemplar. De acuerdo a Coons (1978) el ejemplar que debe ser considerado como holotipo es *Humboldt & Bonpland 3082* (P). El mismo presenta una discrepancia en cuanto a la localidad, pues presenta dos etiquetas: una dice Quito y la otra (que corresponde al año 1833) dice Perú. Por otro lado, Sauer (1967) cita como ejemplar tipo a *Humboldt & Bonpland 156*, aunque aclara que no lo observó. Con respecto a la designación por parte de Sauer del ejemplar *Humboldt & Bonpland 156* como tipo, el propio Sauer, en una carta que le envía a Coons, admite que se trata de un error. El número 156 correspondería al de la página de la edición con que él contaba del *Nova Genera et Species Plantarum*, y que por error se deslizó como el número del ejemplar tipo. Coons sostiene que el holotipo es el ejemplar *Humboldt & Bonpland 3082* y afirma que la etiqueta de la derecha (la de 1833) se debe haber colocado con posterioridad y que por error dice Perú. El Río Guayllabamba al que se refiere Kunth en la diagnosis original está a tan sólo 20 km al NE de Quito, por lo que la etiqueta de la izquierda se corresponde prácticamente con el sitio de colección de este ejemplar.

Ejemplares examinados. ARGENTINA. **Buenos Aires:** Pdo. Berazategui, Hudson, *E. G. Nicora 428* (SI); Pdo. Berisso, Los Talas, *A. L. Cabrera 2790* (LP); Los Talas, *E. Mauri 44* (LP); Pdo. Chacabuco, 1922, *C. L. Spegazzini s.n.* (LP); Pdo. Chascomús, ca. Bahía del Samborombón, sobre puente del Río Samborombón, *E. J. Ringuet 324*, 325 p.p. (ambos en LP); Pdo. Ensenada, *A. L. Cabrera 7459* (LP, SI); Río Santiago, *A. L. Cabrera 10215* (LP); Pdo. Grl. Madariaga, a una legua del pueblo, *A. P. Rodrigo 3527* (LP); Pdo. La Plata, La Plata, *N. D. Bayón 605*, 615, 633, 642 (los cuatro en LPAG); La Plata, 12 abr. 1972, *C. A. de Brizuela s.n.* (LPAG); Bosque, *A. L. Cabrera 5155* (LP); Villa Elisa, *A. L. Cabrera 6312* (LP); Pdo. Magdalena, Atalaya, *C. L. Spegazzini s.n.* (LP-21791); Pdo. Lobería, feb. 1918, *N. Alboff s.n.* (LP); nov. 1873, *C. Berg s.n.* (LP); *A. Scala s.n.* (LP); Pdo. San Fernando, Isla Martín García, *A. Pastore 337* (LP); Pdo. Tapalqué, Ea. El Retiro, feb. 1956, *A. Jurado s.n.* (BA); Pdo. Tigre, Tigre, 1900, *C. L. Spegazzini s.n.* (LP). **Catamarca:** Dep. Ambato, Los Talas, 3 km al S de Los Varela, *C. Saravia Toledo et al. 13038* (CTES); Dep. Belén, Belén, *A. L. Cabrera 1199* (LP); Dep.

Fray Mamerto Esquiú, Piedra Blanca, *B. L. Muller 107* (CTES); Dep. La Paz, El Divisadero, *A. Brizuela 1150* (CTES); Río de La Dorada, *A. Brizuela 970* (CTES); El Milagro, *A. Brizuela 1012* (CTES); El Moreno, *A. Brizuela 1111* (CTES); Dep. Paclín, Cuesta del Totoral, *M. I. H. Scott de Birabén & M. Birabén 1210* (LP); Dep. Santa Rosa, Bañado de Obanta, *Pierotti 99799* (CTES); sin dep. det., El Suncho, *P. Jørgensen 1099* (SI). **Chaco:** Dep. Bermejo, 17 km NNE de La Leonesa, 3 sep. 1973, *A. O. Bordón s.n.* (CTES-408641); Dep. Cmte. Fernández, EEA Sáenz Peña, 29 nov. 1970, *A. O. Bordón s.n.* (CTES-4037); Dep. 12 de Octubre, 10 km O de Hermoso Campo, 21 sep. 1972, *A. O. Bordón s.n.* (CTES-408696, CTES-408701); Dep. Grl. Güemes, 11 km al SSE de Castelli, *A. Schinini & M. Urbani 35778* (CTES); Dep. Mayor L. J. Fontana, Va. Ángela, *P. Boffa 1103* (LP); Dep. Presidencia de la Plaza, 4 km SSO de Pres. de la Plaza, 4 sep. 1972, *A. O. Bordón s.n.* (CTES-410448); 10 km SSO de Pres. de la Plaza, 4 sep. 1972 *A. O. Bordón s.n.* (CTES-410322); Dep. San Fernando, Resistencia, 1886, *C. L. Spegazzini s.n.* (LP). **Ciudad Autónoma de Buenos Aires:** Caballito, *S. Crespo 66* (SI); Flores, *A. T. Hunziker 1458* (LP); Alr., *C. Berg 135* (LP). **Córdoba:** Dep. Capital, NE de Córdoba: La Carolina, a orillas del Río Primero, *A. T. Hunziker 25470* (CORD); Dep. Colón, Sa. Chica, falda E: Unquillo, *A. T. Hunziker 6036*, 6038, 6042, 6043, 6048 (los cinco en CORD); Salsipuedes, *M. Escalante 1*, 60 (ambos en LP); Unquillo, *R. Maldonado 1414* (LP); Dep. Cruz del Eje, San Marcos Sierra, Sa. El Molino, Qda. del Río Calabalumba, *O. Núñez 5* (LP); Dep. Minas, Sa. Guasapampa, falda O, cerca de Ojo de Agua, *A. T. Hunziker 9159* (CORD); Dep. Punilla, Cabalango, antes de Tanti, *A. T. Hunziker 8368* (CORD); Sa. Grande, falda E: Ea. San Bernardo, Ruta Prov. 14, poco antes de Copina, *A. T. Hunziker 11982*, 12022 (ambos en CORD); Dep. Río Segundo, Pilar, *R. Subils 444*, 445 (ambos en CORD); Ea. Exp. Manfredi, *A. Krapovickas 6659* (CORD); *Est. Exp. Manfredi 15* (CORD); Dep. San Alberto, entre San Pedro y El Chocolate, *A. T. Hunziker 11500* (CORD); Sa. Grande, falda O, entre Las Rabonas y Nono, *A. T. Hunziker 11885* (CORD); Dep. San Javier, Sa. Grande, falda O, entre San Javier y Las Rosas, *A. T. Hunziker 11471* (CORD); Dep. San Justo, 2 km al E de Arroyito, *A. Krapovickas et al. 18523* (CTES); Dep. Santa María, Bajo Chico, ca. de Despeñaderos, *A. T. Hunziker 6492*, 6494 (ambos en CORD); Alta Gracia, *A. T. Hunziker 540* (CORD); Dep. Tercero Arriba, Almafuerde, *A. T. Hunziker 6501*, 6502 (ambos en CORD); Almafuerde, *A. T. Hunziker 4924*, 4925 (ambos en CORD); Dep. Totoral, Ruta 9, entre Jesús María y Villa Grl. Mitre, *A. T. Hunziker 12357* (CORD); Dep. Unión, Morrison, *A. T. Hunziker 7323* (CORD); Dep. Tulumba, 14 km al N de San José de la Dormida, *A. Krapovickas et al. 18548* (CTES). **Corrientes:** Dep. Capital, ciudad de Corrientes, *A. Krapovickas & C. L. Cristóbal 15648* (LP); *A. Laffont 10* (LP); *L. Ferraro 552* (CTES); Perichón, *A. Schinini 8727* (CTES); *C. A. Bruno 171* (CTES); Dep. Lavalle, Cnia. Cecilio Echeverría, 10 km al N de Lavalle, *A. Schinini et al. 19254* (CTES); Dep. Mburucuyá, Ea. Santa Teresa, *T. M. Pedersen 1139* (CTES). **Entre Ríos:** Dep. Concordia, Colonia Yeruá, *A. Burkart 21722* (CTES); Dep. Diamante, Diamante, *A. M. Huidobro 2551* (CTES); Dep. Gualeguaychú, Delta del Paraná, Río Ceiba, *A. L. Cabrera 1943* (LP). Gualeguaychú, aeródromo, *A. Burkart et al. 25726* (CTES); Dep. Victoria, entre Diamante y Victoria, *A. Burkart 29314* (CTES); sin dep. det., *M. M. Job 225* (LP). **Formosa:** Dep. Bermejo, Laguna Yema, *N. D. Bayón & C. A. Moreno 835* (LPAG); Dep. Mataros, Ing. G. Juárez, *P. Arenas 2381*

(CTES). **Jujuy:** Dep. Capital, San Salvador de Jujuy, mar. 1903, *C. L. Spegazzini s.n.* (LP); entre León y Nevado de Chañi, Mesada, *H. A. Fabris et al.* 4230 (LP); Lozano, *A. L. Cabrera et al.* 26031 (LP); Caraunco, *A. L. Cabrera et al.* 31523 (SI); Dep. El Carmen, entre Palo Blanco y Pampa Blanca, *A. L. Cabrera et al.* 14601 (LP); Dep. Humahuaca, Alto Sapagua, *C. Saravia Toledo & M. Day* 15255 (CTES); Dep. Ledesma, *A. L. Cabrera & E. M. Zardini* 23869 (LP); Yuto, El Bananal, *H. A. Fabris* 4526 (LP); Dep. Purmamarca, Tascal, *A. L. Cabrera et al.* 15158 (LP); Dep. Santa Bárbara, camino a El Piquete, *A. L. Cabrera & H. A. Fabris* 19912 (LP); Sa. de Santa Bárbara, *H. A. Fabris* 8081 (CTES, LP); camino a Palma Sola, Laguna San Miguel, *A. L. Cabrera & R. Kiesling* 25199 (LP); La Quinta, ca. Laguna de La Brea, *A. L. Cabrera* 4123 (LP); Dep. Tumbaya, Volcán, *A. L. Cabrera et al.* 21753 (LP); Volcán, *A. L. Cabrera et al.* 21755 (LP); Dep. Valle Grande, alr. de Valle Grande, *A. L. Cabrera & H. A. Fabris* 22679 (CTES, LP). **La Rioja:** Dep. Capital, alr. de La Rioja, *G. Covas* 1131 (LP); Dep. Chamental, Chamental, *F. Biurrun & E. Biurrun* 6765 (CTES); Dep. Chilecito, Famatina, 22 mar. 1989, *T. M. Pedersen s.n.* (CTES-381997); Dep. Famatina, Sa. Famatina, Pj. Los Berros, *F. Biurrun et al.* 7148 (CTES); Dep. Laval, Pagancillo, *G. Covas* 1216 (LP); sin dep. det., Sa. Velasco, *J. Morello* 5031 (LP). **Mendoza:** Dep. Luján, Luján de Cuyo, *A. P. Rodrigo* 3115 (LP); Dep. San Rafael, San Rafael, *H. A. Lagiglia* 2035 (LP); Mendoza, Dep. Tupungato, *A. Ruiz Leal* 1216, 2961 (ambos en SI). **Misiones:** Dep. Cainguás, Puerto Rico, *E. Schwindt* 576 (CTES); Dep. Candelaria, Loreto, *J. E. Montes* 2236 (LP); Loreto, *J. E. Montes* 1843, 11176 (ambos en LP); Loreto, *G. C. Giberti & O. Ahumada* 81 (CTES); Santa Ana, *E. Schwindt* 75 (CTES); Santa Ana, *J. E. Montes* 1972 (CTES); Dep. Capital, Posadas, ene. 1907, *C. L. Spegazzini s.n.* (LP); Posadas, *M. Birabén* 5343 (LP); Dep. Eldorado, Ruta Nac. 12, A. Aguaray-Mini, *A. Fernández et al.* 88 (CTES); Dep. Iguazú, Cataratas del Iguazú, *H. R. Descole* 3302 (BAB); Dep. Leandro N. Alem, a 10 km de Cerro Azul camino a Apóstoles, *A. Krapovickas et al.* 15035 (CTES); Dep. San Ignacio, obraje C.M.O., *G. L. Schwarz* 1621 (CTES); Nacanguazú, *G. L. Schwarz* 4659 (CTES); Dep. San Javier, San Javier, *A. L. Cabrera, A. Corte & H. Gebhard* 291 (LP); Alba Posse, *G. L. Schwarz* 4019 (CTES); Santa Rita, *G. Schwarz* 4192 (CTES). **Neuquén:** Chos Malal, Río Barrancas, *O. Boelcke* 4224 (BAB, CTES). **Salta:** Dep. Cafayate, Cafayate, dic. 1896, *C. L. Spegazzini s.n.* (LP); Cafayate, dic. 1898, *C. L. Spegazzini s.n.* (LP); Dep. Capital, Cobos, *A. L. Cabrera & J. M. Marchionni* 12732, 12760 (ambos en LP); Salta, *G. Gerling* 299 (LP); Dep. Cerrillos, La Merced, Finca El Rodeo, 6 km al S de La Merced, *L. J. Novara* 3403 (LP); Dep. Iruya, Iruya, Rodeo Colorado, *M. Figueroa* 28 (LP); alr. de Iruya, *J. A. Hurrell* 719 (LP); Dep. Molinos, Luracatao, Laguna Brealito, *L. J. Novara* 2615 (SI); Dep. Orán, Río San Francisco, ca. de Pichanal, *T. M. Pedersen* 16141 (CTES); Dep. Rosario de Lerma, Valle de Lerma, camino a La Merced, *D. Abbiatti & L. Claps* 18 (LP); Dep. Rosario de Lerma, Río Blanco, *D. Abbiatti & L. Claps* 931; Dep. Santa Victoria, camino al cerro al N de Santa Victoria Oeste, *J. A. Hurrell* 491 (LP); Santa Victoria Oeste, *J. A. Hurrell* 27 (LP); camino de Acoite a Santa Victoria Oeste, *J. A. Hurrell* 442, 444 (ambos en LP); Qda. de Frutayoc, *J. A. Hurrell* 275 (LP); Parque Nacional Baritú, *N. Hilgert* 1917 (CTES). **San Luis:** Dep. Pedernera, Est. San José, Los Manantiales, *E. Scappini* 1705 (CTES). **Santa Fe:** Dep. Gral. Obligado, entre Reconquista y Nicanor Molinas, *M. M. Job* 887 (LP); Villa Ana, *C. Quarín* 652 (CTES); Dep.

Iriondo, entre San José de la Esquina y San Ricardo, *M. Birabén* 66 (LP). **Santiago del Estero:** Dep. Capital, alr. Santiago del Estero, *J. L. Argañaraz* 22 (LP). **Tucumán:** Dep. Capital, Villa Luján, *S. Venturi* 98 (SI); Río Salí, *S. Venturi* 2045 (LP); Dep. Chicligasta, Aconquija, *s. coll.* (LP-76627); Dep. Trancas, Río Tipamayo, *S. Venturi* 4234 (LP); Benjamín Paz, *T. M. Pedersen* 15359 (CTES). **BOLIVIA. La Paz:** oct.–nov. 1912, *O. Buchtien s.n.* (SI). **Santa Cruz:** Prov. Andrés Báñez, 12 km al E de Santa Cruz sobre la ruta a Cotoca, *M. Nee* 33988 (LP). **BRASIL. Santa Catalina:** Aguas de Chapecó, *L. B. Smith & R. M. Klein* 13105 (LP). **Rio Grande do Sul:** entre Morro Tapera y Porto Alegre, *O. Bueno* 1413 (CTES); Uruguayana, *C. L. Spegazzini s.n.* (LP); Santa Cruz do Sul, BR/RS-287, 7 km al N de la ciudad, *T. M. Pedersen* 15909 (CTES). **Paraná:** Mpio. 4 Barras, Río do Corvo, *G. Hatschbach* 21311 (CTES); Mpio. Terra Boa, Fda. Mururé, *G. Hatschbach* 21538, 21540 (ambos en CTES). **CHILE.** Región del Lib. Gral. Bernardo O'Higgins, Rancagua, 1818, *s. coll.* (SGO-048384). **COLOMBIA. Antioquia:** Mpio. Támesis, corregimiento Paraíso, *R. Fonnegra et al.* 2785 (CTES). **ECUADOR. Azuay:** Valle del Río Paute, entre Paute y Cuenca, *W. H. Camp* E-2551 (CTES). **Cañar:** ca. San Marcos, 5–8 km NE de Azogues, *W. H. Camp* 2443 (CTES). **PARAGUAY. Alto Paraná:** Irala, *J. E. Montes* 11110 (LP); Trinidad, Asunción, San Bernardino, *T. Rojas* 1257 (SI). **Amambay:** *T. M. Pedersen* 14777 (CTES); Cerro Corá, 30 km SO de Pedro Juan Caballero, 18 oct. 1986, *T. M. Pedersen s.n.* (CTES). **Central:** Asunción, *P. Arenas* 409 (CTES); Limpio, *E. Bordas* 3962 (CTES); Trinidad, Asunción, Jardín Botánico, *C. Pavetti & T. Rojas* 10439 (SI). **Guaira:** Cordillera de Ybytyruzú, Co. Acatí, *E. M. Zardini & R. Velásquez* 9701 (CTES). **Presidente Hayes:** Cerrito, a 5 km de Benjamín Aceval, *P. Arenas* 209 (CTES). *P. Jörgensen* 3441 (LP, SI). **PERÚ. Huanuco:** *K. Rahn* 286 (CTES). **URUGUAY. Montevideo:** Montevideo, feb. 1865, *Gibert s.n.* (dos ejemplares en LP); A. Miguelete, *F. Rosa-Mato* 418 (LP).

DINAMARCA. København, Islas Brygge, Soyakagefabrik, 4 oct. 1976, *S. Grove s.n.* (CTES).

ESPAÑA. Com. Autónoma de Andalucía: Prov. Cádiz, *T. M. Pedersen* 14923, 14924 (ambos en CTES).

I. 8. *Amaranthus hypochondriacus* L., Sp. Pl. 2: 991. 1753. TIPO: Estados Unidos de América. “Habitat in Virginia”, *Herb. Linnaeus* 1117.24 (lectotipo, designado por Townsend [1985: 25], LINN 1117.24 no visto, imagen!). Figura 11.

Amaranthus frumentaceus Buch.-Ham., Fl. Ind. 3: 609. 1832. TIPO: *Roxburgh s.n.* (holotipo, BR [código de barras] B000000695078 no visto, imagen!).

Amaranthus anardana Buch.-Ham., Numer. List. [Wallich] n. 6903. 1832. TIPO: Zona limítrofe entre India y Nepal. Bihar: Bhâgalpur, material cultivado de semillas blancas, 1828, *N. Wallich* 6903 (holotipo, K [código de barras] K000196859 no visto, imagen!; isotipo, P [cb] P00606388 no visto, imagen!).

Amaranthus hybridus L. var. *erythrostachys* Moq. in de Candolle, Prodr. 13(2): 259. 1849. *Amaranthus chlorostachys* Willd. convar. *erythrostachys* (Moq.) Aellen, Fl. Iranica [Rechinger] 91: 5. 1972. TIPO: “*Amarantus cathecu* hort. Tolos et seminibus Hortis Monspelienensis”, 17 sep. 1844, *s. coll.* (holotipo, P-00307237 no visto, imagen!; isotipo, G-DC [código de barras] G00139326 no visto, imagen!).

Amaranthus leucocarpus S. Watson, Proc. Amer. Acad. Arts. 10: 347. 1875. *Amaranthus leucospermus* S. Watson, Proc. Amer. Acad. Arts. 22: 446. 1887, nom. illeg. *Amaranthus hybridus* L. var. *leucocarpus* (S. Watson) Hunz., Revista Argent. Agron. 10: 340. 1943. TIPO: Estados Unidos de América. Arizona: material cultivado en la Universidad de Harvard de semilla obtenida de aborígenes de Arizona, 1874, *Powell s.n.* (holotipo, GH [código de barras] GH00036999 no visto, imagen!; isotipos, GH [cb] GH00036998 no visto, imagen!, NY [cb] NY00022376!, US [cb] US00106248 no visto, imagen!).

Hierba anual; tallos principales usualmente erectos, 0.4–2(–2.5) m, ramificados arriba, glabros o apenas pubescentes cerca de la inflorescencia cuando jóvenes, glabros al madurar, de color verde o rojizo. Hojas con pecíolo de hasta 6 cm, glabras o glabrescentes, lámina rómbico-ovada hasta ampliamente lanceolada, no ondulada, 4–12 × 2–7 cm, cuneada en la base, cuneada a obtusa en el ápice, mucronada. Inflorescencias principales terminales, espiciformes, rígidas, gruesas y erectas, de color rojo a purpúreo o verdoso, o en espigas axilares; brácteas y bractéolas lanceoladas a linear-subuladas, 3–6(–8) mm, 1.5–2 veces más largas que los sépalos, espinescentes. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con 3 a 5 sépalos lanceolados, 2–2.5 mm, 3 a 5 estambres. Flores pistiladas con 5 sépalos lanceolados a ovado-elípticos o elípticos, 1.3–3(–3.5) mm, agudos en el ápice, uno de la misma longitud o más largo que el fruto, mientras que los restantes son usualmente más cortos, con la vena media marcada y de color pardo; estigmas 3, gruesos, aproximadamente 1.6–1.8 mm, 0.6–0.8 mm de ancho en su base, separándose y abriéndose del centro de la flor. Frutos dehiscentes, con el opérculo rugoso o verrugoso, algunas veces liso, adelgazándose gradualmente hacia la región estigmática formando un rostro largo; semillas de color blancuzco, marfilino, blanco-rosado, rojo oscuro, castaño o negro, 1–1.4 mm diám, lisas y brillantes.

Distribución y ecología. *Amaranthus hypochondriacus* crece ampliamente en el sur de América del Norte, supuestamente su área de origen. Esta especie ha sido ampliamente cultivada como pseudocereal en México (Sauer, 1950, 1967) y en el presente se la cultiva sola o intercalada con maíz (*Palmer 694*, K). En Asia se lo cultiva principalmente como pseudocereal en Afganistán, China, Irán y Nepal, mientras que en Europa y los Estados Unidos de América prima su uso como ornamental. Su cultivo es incipiente en Argentina (Bayón, obs. pers.). Es raro hallarla escapada de cultivo (Mosyakin & Robertson, 2003).

Nombres vulgares. Alegría, bleo, huauhtli (Hunziker, 1943; Sauer, 1967); prince's feather, prince-of-Wales-feather, prince's feather amaranth (Mosyakin & Robertson, 2003).

Discusión. *Amaranthus hypochondriacus* es una especie a veces difícil de identificar al confundírsela por un lado con dos especies silvestres, *A. hybridus* y *A. powellii*, y por el otro con dos especies cultivadas, *A. caudatus* y *A. cruentus*. De estas dos últimas, se diferencia por sus inflorescencias erectas y rígidas, no flácidas ni péndulas. Además, *A. caudatus* presenta en sus flores pistiladas, sépalos internos obtusos o espatulados (no agudos como en *A. hypochondriacus*) e inflorescencia caudada. Por su parte, *A. cruentus* muestra brácteas y bractéolas de 2–3 mm, y el pericarpio del fruto con un estrechamiento abrupto de superficie lisa a modo de rostro, mientras que en *A. hypochondriacus* las brácteas y bractéolas miden 3–6 mm y el adelgazamiento del fruto es gradual y con arrugas. De *A. hybridus* y *A. powellii* se distingue por sus inflorescencias mayores (de más de 30 cm en *A. hypochondriacus*), diferenciándose además de *A. hybridus* porque sus inflorescencias cuentan con ramas rígidas, y brácteas y bractéolas generalmente de mayor longitud.

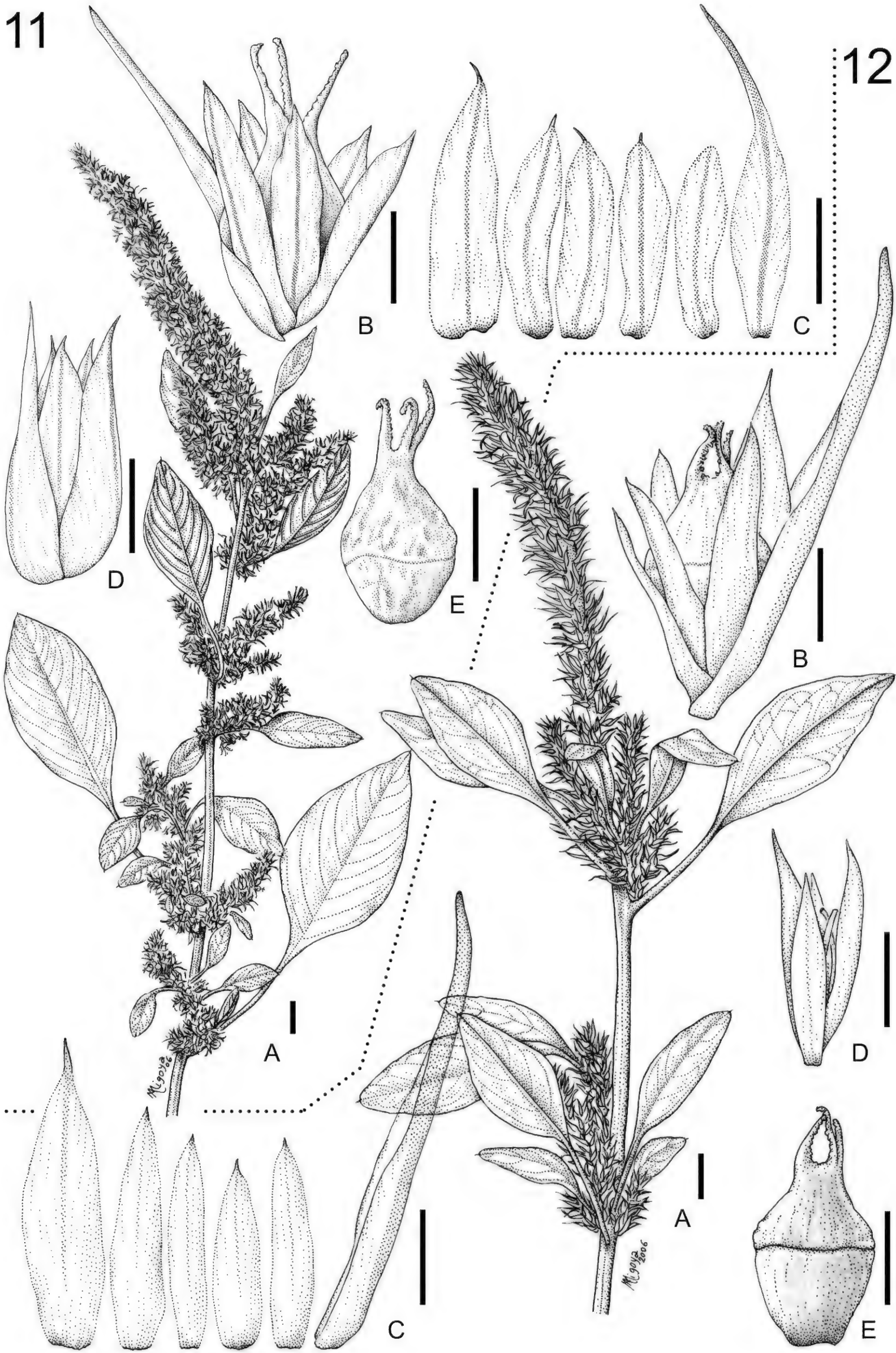
De acuerdo con Sauer (1967, 1976) son dos las hipótesis que podrían explicar el origen de este cultígeno. Por un lado, la hipótesis monofilética considera que la primer especie cultivada que se originó habría sido *Amaranthus cruentus*, la que tuvo su origen en América Central, a partir de *A. hybridus*. Siempre según esta hipótesis, el origen de *A. hypochondriacus* se habría dado a partir del cruzamiento repetido entre *A. cruentus* y *A. powellii*. Por otro lado, la hipótesis polifilética sostiene que *A. hypochondriacus* fue domesticado en México a partir de *A. powellii*.

Ejemplares examinados. ARGENTINA. Pdo. La Plata, camino Gral. Belgrano, entre Villa Elisa y City Bell, *N. D. Bayón 1090* (LPAG).

MÉXICO. **Nuevo León:** Monterrey, 4 oct. 1911, *F. Arsène s.n.* (K). **Jalisco:** Guadalajara, *E. Palmer 694*, 695 (ambos en K).

REINO UNIDO DE GRAN BRETAÑA. Londres: Kew, Cultivated in Hort. Bot. Reg. Kew, seed from México, *R. E. Blakely H3407* (K).

I. 9. *Amaranthus powellii* S. Watson, Proc. Amer. Acad. Arts. 10: 347. 1875. *Amaranthus chlo-rostachys* Willd. var. *powellii* (S. Watson) Priszter, Agrártud. Egyet. Kert-Szölőgazdaságtud. Karának Évk. 2(2): 144. 1953. *Amaranthus retroflexus* L. var. *powellii* (S. Watson) B. Boivin, Naturaliste Canad. 93: 641. 1966. *Amaranthus*



hypochondriacus L. var. *powellii* (S. Watson) Pedersen, Monogr. Syst. Bot. Missouri Bot. Gard. 74: 1245. 1999. *Amaranthus hybridus* L. subsp. *powellii* (S. Watson) Karlsson, Nordic J. Bot. 20: 519. 2000. TIPO: Estados Unidos de América. Arizona: cultivada de semillas traídas desde Arizona por Powell, 1874, *J. W. Powell s.n.* (lectotipo, designado por Iamónico [2014b: 7], US [código de barras] US00106256 no visto, imagen!; isoelectotipos, MO-247671 no visto, imagen!, GH [cb] GH00037008, imagen!, NY [cb] NY01043136 no visto, imagen!, PH [cb] PH00002348 no visto, imagen!). Figura 12.

Amaranthus bracteosus Uline & W. L. Bray, Bot. Gaz. 19: 314. 1894. TIPO: Estados Unidos de América. Nuevo México, 1847, *A. Fendler* 735 (lectotipo, aquí designado, GH [código de barras] GH00036985!; isoelectotipos, BM [cb] BM001024723 no visto, imagen!, GH [cb] GH00036986 no visto, imagen!, MO-1740152 no visto, imagen!).

Amaranthus chlorostachys Willd. var. *pseudoretroflexus* Thell., Vierteljahrsschr. Naturf. Ges. Zürich 52: 443. 1907, as “*Amaranthus chlorostachys* Willd. var. *pseudoretroflexus*”. *Amaranthus hybridus* L. f. *pseudoretroflexus* (Thell.) Thell., Syn. Mitteleur. Fl. 5 (Abth. 1): 239–240. 1919, as “*pseudo-retroflexus*”. *Amaranthus hybridus* L. subvar. *pseudoretroflexus* (Thell.) Thell., Mitt. Bot. Mus. Univ. Zürich 83: 728. 1919. *Amaranthus hybridus* L. var. *pseudoretroflexus* (Thell.) Carretero, Collect. Bot. (Barcelona) 11(4): 125. 1979. TIPO: Suiza. Derendinger, Solothurn, 7 oct. 1907, *Probst s.n.* (holotipo, Z [código de barras] Z000046795 no visto, imagen!).

Amaranthus obovatus S. Watson, Proc. Amer. Acad. Arts. 12: 275. 1877. TIPO: Estados Unidos de América. Nuevo México: Grant Co., copper mines, oct. 1851, *C. Wright* 1748 (holotipo, GH [código de barras] GH00037003 [planta de la izquierda] no visto, imagen!; isotipos, GH [cb] GH00037002 no visto, imagen!, MO-247466 no visto, imagen!).

Hierba anual; tallos principales usualmente erectos, 0.5–1.5(–2) m, simples o ramificados, glabros abajo y pubérulos cerca de la inflorescencia, de color verde o rojizo. Hojas con pecíolos delgados de 1–5 cm, glabras o pubérulas, lámina ovada, ampliamente elíptica a rómbica, rara vez lanceolada, no ondulada, 3–8 × 2–5 cm, cuneada en la base, aguda a obtusa en el ápice, a veces apenas emarginada, con un mucrón de 1–1.2 mm. Inflorescencias terminales y axilares, las primeras espiciformes, 4–25 × 1–2 cm, rígidas,

erectas, poco ramificadas, en este caso con pocas ramas espaciadas y erectas; las segundas en glomérulos o espigas más breves sólo en las axilas foliares distales; brácteas y bractéolas lanceoladas o lineares, 4.5–6(–8) mm, 2–3(–4) veces más largas que los sépalos, espinescentes, muy rígidas. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con 3 a 5 sépalos lanceolado-oblongos, escariosos, agudos, 3 a 5 estambres. Flores pistiladas con 3 a 5 sépalos linear-lanceolados a elípticos, marcadamente desiguales: el externo de 2.2–3 mm mientras que los restantes de 1.2–1.6 mm, con la vena media conspicua sólo en el sépalo mayor, el que supera en longitud al fruto, mientras que el más corto es igual o más corto que el fruto; estigmas tres, 1.9–2.2 mm, engrosados en su base. Frutos dehiscentes o a veces indehiscentes, con el opérculo irregularmente arrugado, 1.5–2 veces más largo que ancho; semillas de color castaño oscuro a negro, ± 1.2 mm, muy brillantes.

Distribución y ecología. *Amaranthus powellii* es originaria del sudoeste de los Estados Unidos de América y del noroeste de México. En el presente se halla naturalizada en regiones templadas de América del Norte, Eurasia y Australia, por lo común en ambientes disturbados, en tierras agrícolas, en caminos y vías férreas, y en orillas de cursos y cuerpos de agua dulce. Crece entre el nivel del mar y los 2500 m (*Polgár* 2453c, SI) (Sauer, 1967; Eliasson, 1987; Mosyakin & Robertson, 2003; Palmer, 2009). Florece entre agosto y noviembre.

Nombres vulgares. Green amaranth, Powell’s amaranth, Powell’s smooth amaranth (Mosyakin & Robertson, 2003).

Discusión. Para Sauer (1967) *Amaranthus powellii* sería progenitora de la especie cultivada *A. hypochondriacus*. Ambas tienen inflorescencias rígidas y erectas, con brácteas y bractéolas fuertes, espinescentes y sépalos de las flores pistiladas agudos en el ápice. Se diferencian porque *A. hypochondriacus* tiene inflorescencias mayores de 30 cm de longitud, generalmente vivamente coloreadas de rojo, púrpura o amarillo, siendo sus semillas de color claro. Una especie silvestre que se le asemeja es *A. hybridus*, aunque sus brácteas y bractéolas son un tanto menores (2–4 mm), sus

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Figura 11. *Amaranthus hypochondriacus* L. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A–E, ilustrado de *Powell s.n.* (NY). La barra de escala para A = 1 cm; para B–E = 1 mm.

Figura 12. *Amaranthus powellii* S. Watson. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A, ilustrado de *Pedersen* 9789 (LP); B–E, de *Polgar* 2453 (SI). La barra de escala para A = 1 cm; para B–E = 1 mm.

inflorescencias flácidas con sus ramas no tan erectas ni tan próximas al eje. Por sus inflorescencias espiciformes poco ramificadas, brácteas y bractéolas mucho mayores que los sépalos de las flores pistiladas, y los frutos dehiscentes, *A. powellii* se parece *A. viscidulus*, pero esta última presenta plantas algo carnosas con pubescencia glandulosa.

Uline y Bray (1894b) describen a *Amaranthus bracteosus* sobre la base del ejemplar *Fendler 735*, citando asimismo el año 1847 como fecha de colección. Se han encontrado cuatro materiales asociados a la diagnosis original, dos de los cuales se hallan depositados en GH, otro en BM y otro en MO. Se ha tenido la oportunidad de estudiar el ejemplar GH [código de barras] GH00036985 que presenta tallos con hojas e inflorescencias bien desarrolladas que responden a la diagnosis original, por lo que es designado como lectotipo de *A. bracteosus*.

La cartulina del tipo de *Amaranthus obovatus* C. Wright 1748 (GH) contiene dos plantas: la de la derecha (GH [código de barras] GH00037004) corresponde al isotipo de *A. wrightii*, mientras que la de la izquierda (GH [cb] GH00037003) al holotipo de *A. obovatus*. En las inflorescencias de la última se aprecia claramente que el tamaño de las brácteas y bractéolas superan los 4.5 mm.

Pedersen (1999) sostiene que *Amaranthus powellii* está presente en Argentina al mismo tiempo que propone una nueva combinación: *A. hypochondriacus* L. var. *powellii* (S. Watson) Pedersen. Cita al ejemplar *Kiesling 6998* (SI) en el que se observa que las brácteas y bractéolas florales son espinescentes y de alrededor de 4 mm de longitud, lo que se corresponde con *A. hybridus* subsp. *hybridus* y no con *A. powellii*, por lo que se propone excluir a este último taxón de la flora argentina.

Thellung (1907) sostiene que *Amaranthus chlorostachys* Willd. var. *pseudoretroflexus* Thell. se caracteriza por tener brácteas y bractéolas de 5 mm (o mayores), por tener sépalos de las flores pistiladas de igual longitud o más largos que los frutos y la existencia de tres o cuatro estambres en las flores estaminadas. No he tenido acceso al material tipo, ni a la diagnosis original. Sin embargo, los caracteres citados por el autor de la variedad se corresponden con los de *A. powellii*.

Ejemplares examinados. MÉXICO. **Durango:** ciudad de Durango, *E. Palmer 759* (K).

HUNGRÍA. Syör, S. *Polgár 2453 b, 2453c* (ambos en SI).

ESTADOS UNIDOS DE AMÉRICA. **Idaho:** Coeur D'Alene Mtns., *J. B. Leiberger 1550* (K).

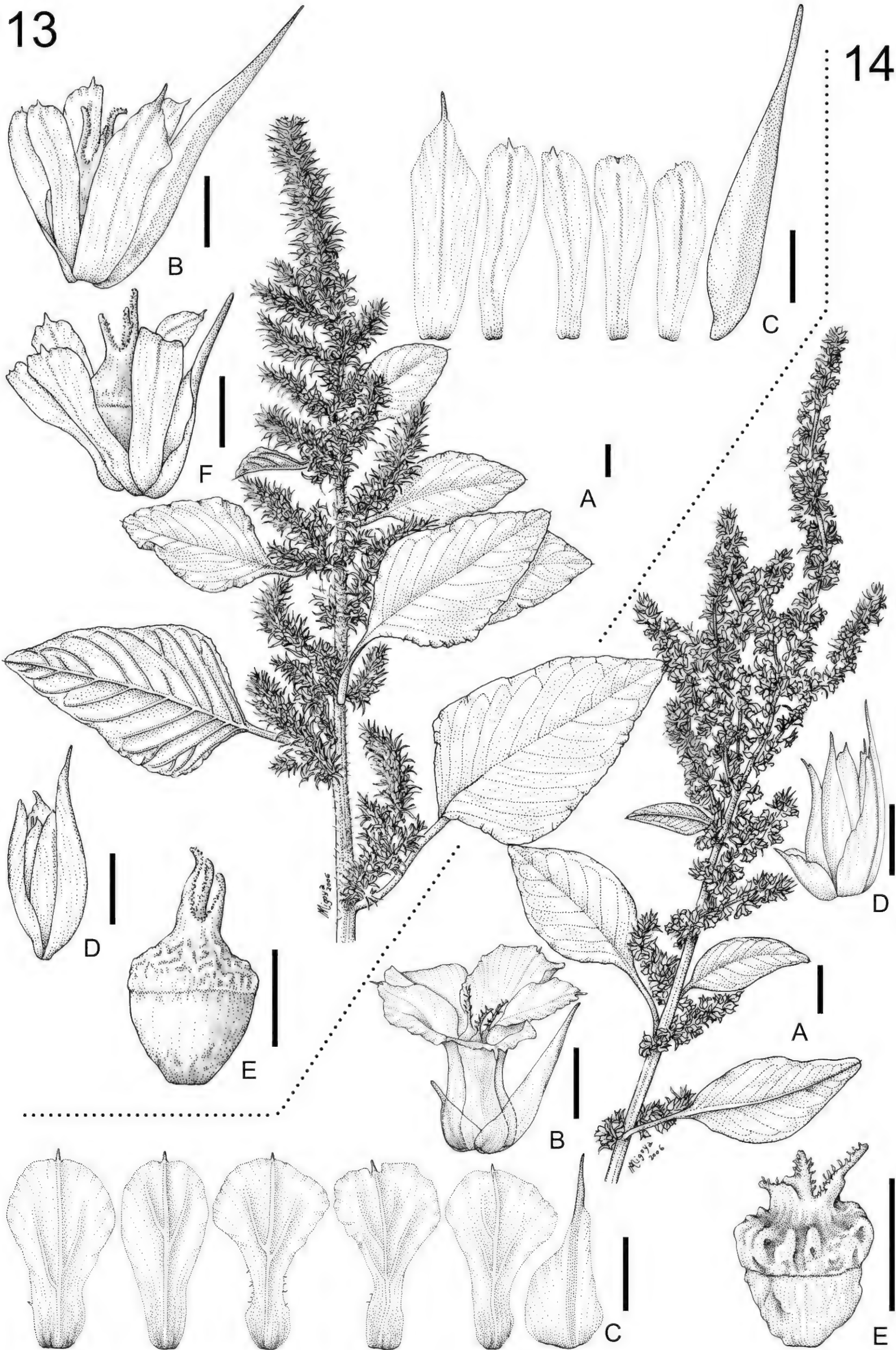
I. 10. *Amaranthus retroflexus* L., Sp. Pl. 991. 1753.
Galliardia retroflexa (L.) Nieuwl., Amer. Midl. Naturalist. 3: 278. 1914, comb. inval. [*Galliardia* Bubani, nom. nud.]. TIPO: Suecia. Cultivado en Uppsala, "Habitat in Pensylvania. Kalm", [desde protólogo]. *Herb. Linnaeus 1117.22* (lectotipo, designado por Townsend [1974a: 12], LINN 1117.22 no visto, imagen!). Figura 13.

Amaranthus retroflexus var. *salicifolius* I. M. Johnston, J. Arnold Arbor. 25: 157. 1944. TIPO: México. Coahuila: 12 mi. O de Saltillo, Parras, jun. 1880, *E. Palmer 2043* (holotipo, GH [código de barras] GH00037030 no visto, imagen!).

Hierba anual; tallos principales erectos, usualmente con ramas ascendentes, de hasta 1(–2) m, pero muy a menudo más bajos, \pm densamente pubescentes debajo y en la inflorescencia. Hojas con pecíolo de hasta 5 cm, pubescentes cuando jóvenes en la cara abaxial, con algunos pelos sobre los nervios principales cuando adultas, lámina ovada, oblongo-ovada o rómbica, no o algo ondulada, 3–8(–10) \times 1.5–4(–6.5) cm, atenuada a cuneada en la base, obtusa o subaguda en el ápice, a menudo retusa, con mucrón de 0.4–0.8 mm. Inflorescencias terminales y axilares espiciformes, cortas, anchas y densas, las primeras lobadas y formando panojas cortas, no superando los 35 cm, de colores verdosos o blancuzcos; brácteas y bractéolas lanceoladas, espinescentes, 3.5–5(–6) mm, 1–2 veces más largas que los sépalos, ápice con arista de hasta 2 mm. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con (4–)5 sépalos oblongo-elípticos, 1.5–3 mm, apenas retusos o con un mucrón de hasta 0.4 mm, 5 estambres. Flores pistiladas con 5 sépalos oblongo-espatulados a espatulados, 1.5–3.5 mm, redondeados, truncados o emarginados en el ápice, con la vena media verdosa que no alcanza al ápice, mucho más largos que el fruto; estigmas tres, 0.5–1 mm, delgados, erguidos. Frutos dehiscentes, opérculo rugoso, gradualmente adelgazado hacia la zona estigmática; semillas de color castaño-negruzco, 1–

Figura 13. *Amaranthus retroflexus* L. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. —F. Flor pistilada con bráctea breve. A–E, ilustrado de Bayard Long 61638 (SI); F, de Polgar 2708b (LP). La barra de escala para A = 1 cm; para B–F = 1 mm.

Figura 14. *Amaranthus scariosus* Benth. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A–E, ilustrado de Hammel 19403 (K). La barra de escala para A = 1 cm; para B–E = 1 mm.



1.2 mm, muy brillantes en el centro, más opacas y reticuladas en el área marginal.

Distribución y ecología. *Amaranthus retroflexus* es nativa del centro y este de América del Norte, pero convertida en maleza en amplias áreas de todos los continentes. Se la encuentra en tierras no cultivadas, en orillas de cursos de agua, así como en campos de regadío, en jardines, vías férreas, banquinas de caminos y lugares donde se arrojan desperdicios. Esta especie crece entre el nivel del mar y los 2500 m (Bayard Long 61638, SI) (Hunziker, 1966; Mosyakin & Robertson, 2003; Palmer, 2009). En el hemisferio norte florece entre los meses de junio y octubre.

Nombres vulgares. Bledo, moco de pavo, penacho (de la Peña & Pensiero, 2004); redroot pigweed, redroot amaranth, wild beet amaranth, rough pigweed, common amaranth (Mosyakin & Robertson, 2003).

Discusión. *Amaranthus retroflexus* se asemeja a *A. wrightii*, *A. scariosus* y *A. hybridus* subsp. *quitensis* por presentar en sus flores pistiladas todos o al menos algunos de sus cinco sépalos obtusos, redondeados o emarginados apicalmente. Dos diferencias que permiten distinguir a *A. retroflexus* de esas tres especies son que tiene sus tallos conspicuamente pubescentes cerca de la inflorescencia y que el (o los) sépalos internos de las flores pistiladas tienen la vena media interrumpida, no llegando al ápice de los mismos.

Ejemplares examinados. ARGENTINA. **Córdoba:** Dep. Punilla: Sa. Grande, Ea. San Bernardo, A. T. Hunziker 11628, 11997, 12000, 12021, 12034 (los cinco en CORD); Sa. Chica, Molinari, Ea. San Jorge, A. T. Hunziker 13442 (CORD).

BÉLGICA. **Flandre-Orientale:** Drongen, H. Stieperaere B2490 (CTES, LIL). BULGARIA. Sofía, in ruderalis prope urb., N. Vyhodcevski 433 (SI). ESPAÑA. **Alicante:** Pego, Sa. de Mustalla, Cona del Rull, a 10 km del Mar Mediterráneo, A. Schinini 31074 (CTES). **Castilla:** Burgos, Miranda de Ebro, Elías 4150 (SI). **Cataluña:** Barcelona, Manlleu, champs, à la Devèse, Gonzalo 6889 (SI); Barcelona, Gonzalo 5540 (SI); Manlleu, Gonzalo 5937, 6323 (ambos en SI); Manlleu, camps, F. Sennen 5539 (SI). FRANCIA. **Mid Pyrénées:** Heranet, Castelnau-le-Lez, G. Blanchet 17 (CTES). HUNGRÍA. Syör Süterbahvhof, S. Pólgar 1754, 2708b (ambos en SI). PORTUGAL. **Extremadura:** Lisboa, alr. Sa. Monsanto, ago. 1890, A. R. da Cunha s.n. (SI). REPÚBLICA CHECA. **Bohemia centralis:** Praga-Troja, M. Deyl 18492 (LIL). RUMANIA. Oltenia, D. Cîrtu & I. Teodorescu 918, 919 (ambos en BAB); Bacău, D. Mititelu et al. 511 (BAB). SUIZA. **Tessin:** Malvaglia, T. M. Pedersen 7936 (CTES, LP); Zürich, Gemeinde Rümlang-Kloten, 15 sep. 1947, H. Bühner s.n. (CTES).

CANADÁ. **British Columbia:** E. W. Tisdale 40-356 (BAB). **Québec:** Ottawa, Carleton Co., W. H. Minshall 2439 (LP); Ottawa, H. A. Senn et al. 967 (LP). ESTADOS

UNIDOS DE AMÉRICA. **Illinois:** Peoria Co., Alley, Peoria Heights, V. H. Chase 10780 (LIL). **Nuevo México:** Sa. Co., O. B. Metcalfe 1342 (LIL). **Pennsylvania:** Bucks Co., Bayard Long 61638 (SI). **Wisconsin:** Rock Co., costa SE del Lago Koshkonong, H. H. Iltis & J. J. Janecek 8449 (LIL).

I. 11. *Amaranthus scariosus* Benth., Bot. Voy. Sulphur 158. t. 51. 1844. *Sarratia scariosa* (Benth.) Moq. in de Candolle, Prodr. 13(2): 269. 1849. TIPO: Honduras. Mpio. Amapala, Dep. de Valle: Tiger Island, Golfo de Fonseca, *Sinclair s.n.* (lectotipo, designado por Nelson Sutherland [1996: 56], K [código de barras] K000449031 no visto, imagen!). Figura 14.

Hierba anual; tallos principales erectos, de hasta 2.5 m, ramificados, glabros. Hojas con pecíolo de 2–4 cm, glabras, lámina ovada, ovado-lanceolada o elíptica, no ondulada, 4–6 × 2.5–3.2 cm, cuneada en la base, adelgazándose gradualmente hacia el ápice, este desde subagudo a obtuso, mucrón 1 mm. Inflorescencias terminales, formando una panoja, 10–30 × 3–5 cm, o axilares en glomérulos de 1 cm diám; brácteas y bractéolas ovado-deltoides, 2.3–3.7 mm, apenas más largas que los sépalos, espinescentes, ápice acuminado, con arista de 0.5–0.75 mm. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con 5 sépalos lanceolados, 2–3 mm, con su vena media marcada, acuminados, 5 estambres. Flores pistiladas con 5 sépalos, obovados o espatulados, a veces emarginados, 2.3–3 mm, mucronados o no, con la vena media pinnada, esponjosos en la base; estigmas tres, 0.5–1 mm. Frutos dehiscentes, con arrugas verticales en la urna, rugosos en el opérculo, más cortos que los sépalos; semillas de color negro en el área central y castaño en el área marginal, 0.8 × 1 mm, punteadas en el centro y lisas en el margen.

Distribución. Costa occidental de México y América Central. Florece entre los meses de octubre y mayo.

Discusión. *Amaranthus scariosus* se asemeja a la especie australiana *A. pallidiflorus* F. Muell. (*Amaranthus* subg. *Albersia*), cuando los ejemplares de *A. scariosus* muestran una inflorescencia espici-forme apical, ramificada, grande y blanquecina. Se diferencia porque *A. scariosus* tiene: 1) brácteas y bractéolas iguales o mayores que los sépalos de las flores pistiladas (no de ± la mitad) y 2) flores estaminadas con cinco estambres (no tres o cuatro). Sus flores pistiladas tienen un aspecto exterior urceolado, aunque en rigor no lo son pues sus sépalos se hallan libres, no soldados como ocurre en varias especies de *Amaranthus* subg. *Albersia* (*A.*

anderssonii, *A. hunzikeri*, *A. kloosianus*, *A. polygonoides*, *A. squamulatus* y *A. urceolatus*). Sin embargo, todas estas últimas especies tienen hojas menores de 2 cm de ancho (en *A. scariosus* superan los 2.5 cm de ancho), ni inflorescencias terminales del tamaño de *A. scariosus*. Además, *A. scariosus* tiene frutos siempre dehiscentes, lo que se observa sólo en *A. hunzikeri* y rara vez en *A. squamulatus*.

Ejemplares examinados. COSTA RICA. **Cordillera de Guanacaste:** Cantón de Liberia, faja costera del Golfo de Papagayo, Puerto Culebra, *B. Hammel et al.* 19403 (K); San José de Costa Rica, *A. Tonduz* 13704 (K). MÉXICO. **Guerrero:** Acapulco, *E. Palmer* 142 (K).

I. 12. *Amaranthus spinosus* L., Sp. Pl. 991. 1753.
Galliardia spinosa (L.) Nieuwl., Amer. Midl. Naturalist 3: 278. 1914, comb. inval. [*Galliardia* Bubani, nom. nud.]. TIPO: "Habitat in Indiis", *Herb. Linnaeus* 1117.27 (lectotipo, designado por Fawcett & Rendle [1914: 130], LINN 1117.27 no visto, imagen!). Figura 15.

Hierba anual; tallos principales erectos, 0.3–1.5 m, ramificados, glabros a pubescentes en la parte distal de la planta, especialmente cerca de la inflorescencia. Hojas con pecíolo de hasta 7 cm, glabras o glabrescentes, con 2 espinas divaricadas en la axila, de hasta 15 mm, de color verdoso con el ápice pajizo, lámina ovada, lanceolada u oblonga, a menudo rómbica, no ondulada, 2–8 × 0.7–3 cm, atenuada en la base, obtusa o apenas emarginada en el ápice, con mucrón de 1–1.2 mm. Inflorescencias terminales en panoja, con ramas espiciformes, de color verdoso, o axilares, en glomérulos, a menudo con espinas; brácteas y bractéolas ovadas a ovado-deltoides, con una arista corta y prominente, formada por la vena media excurrente, usualmente más cortas que los sépalos, pero algunas veces iguales o apenas más largas. Flores de los glomérulos axilares enteramente pistiladas, mientras que la inflorescencia terminal presenta sus cimas apicales estaminadas y las basales pistiladas. Flores estaminadas con 5 sépalos oblongo-elípticos a oblongo-obovados, iguales o subiguales, atenuados en el ápice con la vena media excurrente, 5 estambres. Flores pistiladas con 5 sépalos espatulado-oblongos, iguales o subiguales, obtusos, mucronulados; estigmas tres, 1–1.4 mm, con las bases engrosadas. Frutos dehiscentes, lisos o rugosos, del largo de los sépalos; semillas de color negruzco, 0.8–1.1 mm, brillantes.

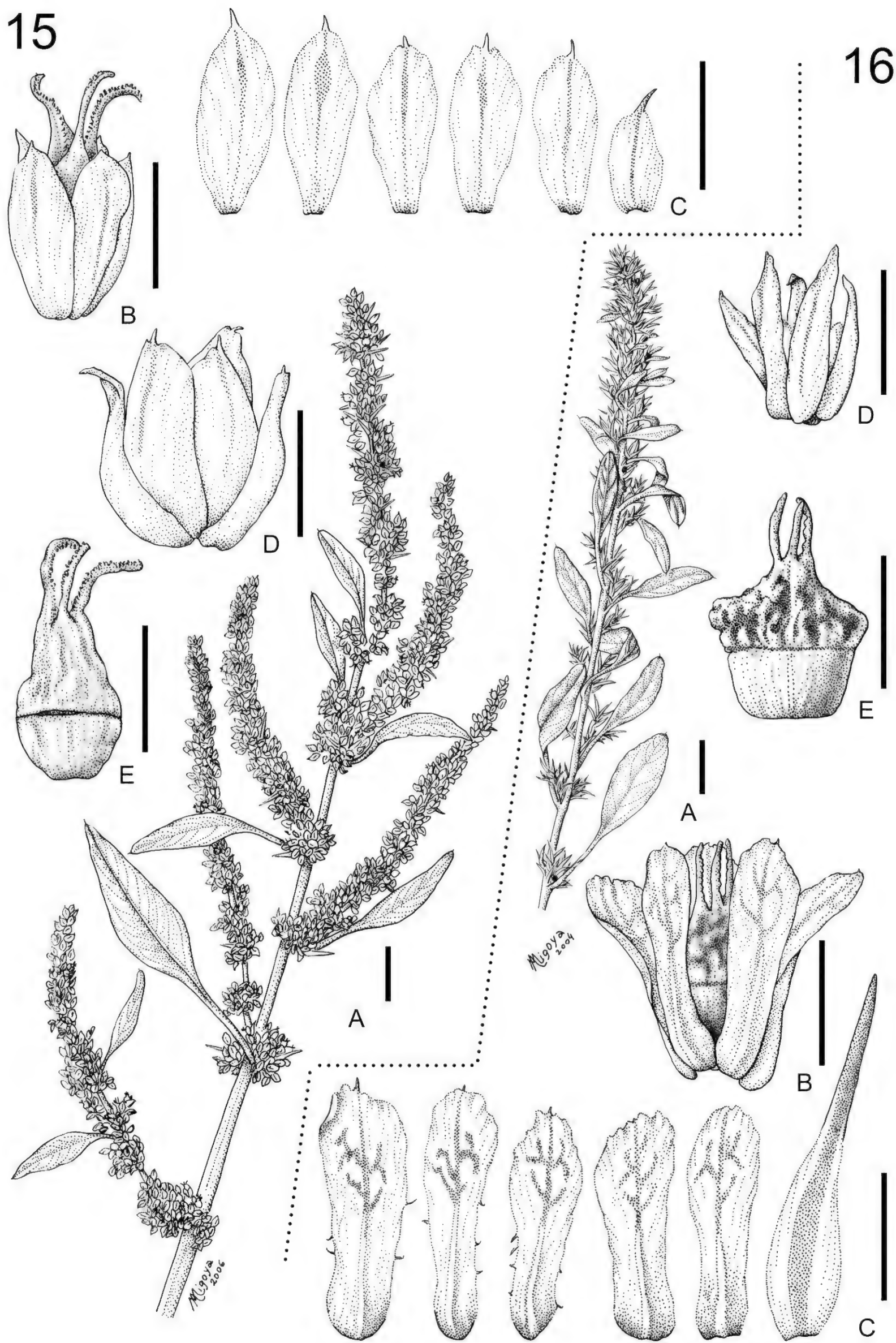
Distribución y ecología. *Amaranthus spinosus* es originaria de las zonas tropicales bajas de América. Esta especie se encuentra desde el centro de Estados Unidos hasta Argentina. Planta ruderal (*Cabrera* 10872, LP) que en la actualidad constituye

una maleza (*Lurvey* 543, CTES) de distribución cosmopolita, principalmente en regiones tropicales y templado-cálidas (Eliasson, 1987; Carrizo & Isasmendi, 1998). Crece entre el nivel del mar y los 1800 m.

Nombres vulgares. Ataco, ataco casa (Carrizo & Isasmendi, 1998); ataco, ataco casha (Macbride, 1937); ataco espinudo (de la Peña & Pensiero, 2004); spiny amaranth, thorny amaranth (Mosyakin & Robertson, 2003).

Discusión. *Amaranthus spinosus* es una especie fácil de distinguir en el material de herbario por su par de espinas axilares. Otro rasgo particular de *A. spinosus* es la separación que existe entre las flores pistiladas (ubicadas en los glomérulos axilares y en la porción basal de las inflorescencias terminales) y las estaminadas (ubicadas en el ápice de las inflorescencias terminales).

Ejemplares examinados. ARGENTINA. **Chaco:** Dep. 1° de Mayo, Margarita Belén, *A. G. Schulz* 2952 (CTES); Colonia Benítez, *A. G. Schulz* 8671 (CTES). **Corrientes:** Dep. Santo Tomé, Ea. Rincón de las Mercedes, *T. M. Pedersen* 5424 (CTES). **Jujuy:** Dep. Capital, Los Blancos, *T. M. Pedersen* 10756 (CTES); Dep. Santa Bárbara, Aguas Calientes, *A. L. Cabrera et al.* 31416 (CTES); El Palmar, *O. Ahumada & A. Castellón* 4910 (CTES). **Misiones:** Dep. Guaraní, predio Guaraní, sector CIFOR, *H. A. Keller* 133 (CTES); Dep. Iguazú, Río Uruguai, 5 oct. 1949, *V. R. Perrone s.n.* (BA); Puerto Península, *A. Krapovickas et al.* 18365 (CTES); Dep. Lib. Grl. San Martín, Puerto Leoni, *A. L. Cabrera et al.* 234 (LP); Dep. San Javier, San Javier, *A. L. Cabrera et al.* 289 (LP); Dep. San Pedro, Salto Moconá, *L. Mroginski & S. M. Pire* 806 (CTES); Pj. Paraíso, aldea aborigen Guavirá Poty, *H. A. Keller* 1341 (CTES). **Salta:** Dep. Grl. San Martín, entre Cnel. Cornejo y Río Seco, *A. L. Cabrera et al.* 34408 (CTES, LP); Dep. La Caldera, Río Vaqueros, ca. puente sobre Ruta 9, *L. J. Novara* 8789 (CTES); Dep. Orán, Vespucio, *A. L. Cabrera* 4179 (LP); 15 km O de Aguas Blancas, *H. A. Fabris & J. V. Crisci* 7325 (LP); Vespucio, alr. del campamento de YPF, *D. Abbiatti & L. Claps* 230 (LP). **Tucumán:** Dep. Chicligasta, Cochuna, *O'Donnell* 84 (LP); Dep. Tafí, Portezuelo, *R. Rocha* 3689 (CTES). BOLIVIA. **Beni:** Prov. Ballivián y Yacuma, *J. Valderrama* 34 (CTES); Prov. Marbán, San Rafael, *G. Beck* 2713 (CTES). **La Paz:** Prov. Sud Yungas, Alto Beni, Popoy, *R. Seidel* 2020 (CTES). **Pando:** Prov. Manuripi, Playa Cairo, *M. Moraes* 433 (CTES). **Santa Cruz:** San Pedro, *F. E. Tollewey* 103 (CTES). BRASIL. **Amapá:** Macapá, *B. V. Rabelo et al.* 3298 (CTES). **Mato Grosso:** Mpio. de Poconé, faz. Nova Berlim, 85 km al S de Poconé, *M. Schessl* 131291-1-2 (CTES). **Mato Grosso do Sul:** Corumbá, *V. J. Pott* 167 (CTES). **Minas Gerais:** entre Ouro Preto y Ponte Nova, *L. Badini* 24014 (CTES). **Pará:** Conceição de Araguaia, 20 km al O de Redenção, *T. Plowman* 8811 (CTES). **Paraná:** Curitiba, Caiobá-Paraná, *N. Imaguire* 306 (CTES); Mpio. Paranagua, Pôrto D. Pedro II, *G. Hatschbach & O. Guimarães* 21443 (CTES); Río Ivaí, Barra Río Claro, *G. Hatschbach* 21530 (CTES). **Piauí:** Paranaíba, Boqueirão, *M. S. Bona Nascimento* 25 (CTES). **San Pablo:** Santos, jun. 1912, *C. L. Spegazzini s.n.* (LP). **Santa Catarina:** ca. Itapiranga, *T. M. Pedersen* 13708 (CTES). COLOMBIA.



Valle del Cauca: La Cumbre, ca. de la hacienda “La Sofía”, *J. E. Ramos* 790 (CTES). ECUADOR. **Chimborazo:** Cañón del Río Chanchan ca. de Huigra, *W. H. Camp* E-2966 (CTES). PARAGUAY. **Alto Paraná:** Irala, *J. E. Montes* 11118 (LP); Santa Rosa, *L. C. Stutz* 521 (CTES). **Itapúa:** Encarnación, *E. Lurvey* 543 (CTES). PERÚ. **Lima:** Boza, *A. L. Cabrera* 10872 (LP). **Junín:** San Ramón, *A. L. Cabrera* 10935 (LP). VENEZUELA. **Anzoátegui:** Dpto. Peñalver, Mpio. Sucre, a orillas del Río Unare, *A. Castillo & A. De Franca* 2635 (CTES).

MÉXICO. **Chiapas:** Mpio. Ocozocoautla de Espinoza, Presa de Malpaso, *A. Shilom Ton* 3300 (CTES). **Michoacán:** Parácuaro, *J. C. Soto Núñez et al.* 8004 (CTES).

PANAMÁ. **Los Santos:** en la naciente del Río Pedregal, 37 km al SW de Tonosí, *W. H. Lewis* 2975 (CTES). **Panamá:** Cerro Azul, *C. Castrejón* 25 (CTES); Cerro Azul, *L. Medina* 37 (CTES).

FRANCIA. **Ht.-Rhin:** Baumwollkompost in Isseinheim, *P. Aellen & W. Baumgartner* 25 (CTES).

I. 13. *Amaranthus wrightii* S. Watson, Proc. Amer. Acad. Arts 12: 275. 1877. TIPO: Estados Unidos de América. Nuevo México: Grant Co., copper mines, 11 oct. 1851, *C. Wright* 1748 (lectotipo, aquí designado, GH p.p. [planta de la derecha] [código de barras] GH00037019 no visto, imagen!; isolectotipos, US [cb] US00106269 no visto, imagen!, GH [cb] GH00037004 no visto, imagen!, K [cb] K000190110 no visto, imagen!, K [cb] K000190111 no visto, imagen!, MO no visto, imagen!). Figura 16.

Hierba anual; tallos principales erectos o ascendentes, 0.2–1 m, simples o ramificados, glabros, de color blancuzco o rojizo. Hojas con pecíolo de 5–40 mm, glabras, lámina lanceolada a ovado-rómbica, no ondulada, 1.5–6 × 0.5–3 cm, atenuada o cuneada en la base, aguda a obtusa en el ápice, apenas emarginada, apenas discolora, mucrón 0.8–1.2 mm. Inflorescencias terminales y axilares, las primeras en espigas densas simples o ramificadas, 4–25 × 1–1.5 cm, fuertes, erectas, a menudo foliosas, interrumpidas en la base, de color verdoso con tintes de color rosado; las segundas en glomérulos densos, de hasta 1 cm diám; brácteas y bractéolas linear-lanceoladas, 1.5–4 mm, hasta doblando en longitud a los sépalos, espinescentes. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con 5 sépalos oblongos, agudos, (3–)4–5 estambres. Flores pistiladas con 5 sépalos oblongos, oblongo-espátulados u oblongo-obovados, 1.5–2 mm, algo adelgazados en su

base, redondeados o truncados en el ápice, a menudo retusos a emarginados (a veces el sépalo externo subagudo y espinescente), con una vena marcada que por lo general llega al ápice, ramificada, erectos, muy próximos en la base pero sin llegar a soldarse; estigmas tres, 0.5 mm, delgados. Frutos dehiscentes, 1.3–2 mm, urna lisa, opérculo liso o rugoso, menores o iguales a los sépalos; semillas de color castaño-rojizo muy oscuro a negro, 0.9–1 mm, brillantes en el centro y punteadas en la zona marginal.

Distribución y ecología. Norte de México y sudoeste de U.S.A. En ambientes disturbados naturalmente, orilla de cursos de agua, cañones y semidesiertos. Crece entre los 500 m y los 2000 m (Mosyakin & Robertson, 2003).

Nombre vulgar. Wright’s amaranth (Mosyakin & Robertson, 2003).

Discusión. *Amaranthus wrightii* es una especie muy cercana a *A. retroflexus* por los sépalos de las flores pistiladas en número de cinco, obtusos, emarginados o retusos apicalmente. Se distingue de dicha especie por ser glabra o glabrescente y porque los sépalos de las flores pistiladas tienen la vena media llegando hasta el ápice (salvo en el sépalo externo). Tiene cierta semejanza también con *A. torreyi*, pero esta especie posee sépalos más estrechos en la base, adelgazándose en una uña.

Watson (1877: 275) menciona lo siguiente en el protólogo de *Amaranthus wrightii*: “Collected at the Copper Mines, by Mr. Wright (n. 1748, in part), October, 1851; also in the Upper Arkansas Valley, by Messrs. Wolf & Rothrock (n. 275) in 1873”. Probablemente Watson haya tenido en sus manos esta cartulina al describir la especie. Estos dos ejemplares están montados sobre una misma cartulina, estando ubicado el primero a la derecha, GH [código de barras] GH00037019, y el segundo a la izquierda, GH [código de barras] GH00037020. Del primero existen duplicados depositados en el mismo GH, K[2], MO y US, mientras que del segundo se ha localizado uno en US. El ejemplar *Wright* 1748 (GH00037019) consta de una planta completa, que se corresponde con el protólogo por lo que es elegida como lectotipo de *A. wrightii*.

Finalmente, conviene aclarar que el segundo ejemplar de GH también cuenta con dos plantas

←
Figura 15. *Amaranthus spinosus* L. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A, ilustrado de *Cabrera* 10872 (LP); B–E, de *Cabrera* 10931 (LP). La barra de escala para A = 1 cm; para B–E = 1 mm.

Figura 16. *Amaranthus wrightii* S. Watson. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A, ilustrado de *Wright* 1748 (K); B–E, de *Green s.n.* (K). La barra de escala para A = 1 cm; para B–E = 1 mm.

montadas en una misma cartulina, la de la derecha corresponde a *Amaranthus wrightii* GH [código de barras] GH00037004, mientras que la de la izquierda al isotipo de *A. obovatus* GH [cb] GH00037003.

Ejemplares examinados. ESTADOS UNIDOS DE AMÉRICA. **Colorado:** Upper Arkansas Valley, *J. Wolf* 275 (sintipo, *Amaranthus wrightii*, US [código de barras] US01169683 no visto, imagen!). **Nuevo México:** near Silver City, 30 sep. 1880, *E. L. Greene s.n.* (K).

II. *Amaranthus* L. subg. *Albersia* (Kunth) Gren. & Godr., Fl. France 3(Pt. 1): 3. 1855. Basónimo: *Albersia* Kunth, Fl. Berol. 2: 144. 1838. TIPO: *Amaranthus blitum* L. [= *Albersia blitum* (L.) Kunth]. Figura 17.

Bliton Adanson, Fam. 2: 506. 1763. *Dimeianthus* Raf., Fl. Tellur. 3: 41-42. 1837. TIPO: no designado.

Amaranthus secc. *Blitopsis* Dumort., Fl. Belg. (Dumortier) 19. 1827, p.p., sp. excl. TIPO: *Amaranthus blitum* L. (lectotipo, designado por Carretero [1985: 284]).

Amblogyna Raf., Flor. Tellur. 3: 42. 1837. *Roemeria* Moench., Methodus 341. 1794, hom. illeg., non *Roemeria* Medik., Ann. Bot. (Usteri) 1 (3): 15. 1792. TIPO: *Amaranthus polygonoides* L. [= *Amblogyna polygonoides* (L.) Raf.].

Euxolus Raf., Fl. Tellur. 3: 42. 1837. TIPO: *Amaranthus deflexus* L. [= *Euxolus deflexus* (L.) Raf.].

Pentrius Raf., Fl. Tellur. 3: 42. 1837. *Euxolus* Raf. secc. *Pentrius* (Raf.) Moq. in de Candolle, Prodr. 13(2): 273. 1849, nom. inval. [nom. prov., cf. Art. 36.1 (b)].

Mengea Schauer, Nov. Actorum. Acad. Caes. Leop.-Carol. Nat. Cur. 19(Suppl. 1): 405. 1843. TIPO: *Amaranthus peruvianus* (Schauer) Standl. [= *Mengea peruviana* Schauer].

Sarratia Moq. in de Candolle, Prodr. 13(2): 233, 268-269. 1849, p.p. excl. typ. [Véase la discusión sobre la lectotipificación del género *Sarratia* en el tratamiento de *Amaranthus* subg. *Amaranthus*.].

Amaranthus secc. *Pyxidium* Moq. in de Candolle, Prodr. 13(2): 262. 1849. *Amaranthus* secc. *Blitopsis* sensu auct. plur., p.p. TIPO: *Amaranthus tricolor* L.

Galliaria Bubani, Fl. Pyren. 1: 184-185. 1897, nom. nud.

Euxolus Raf. secc. *Pentamorion* Beck., Icon. Fl. Germ. et Helv. 24: 182. 1909. *Amaranthus* secc. *Pentamorion* (Beck) Mosyakin & K. R. Robertson, Ann. Bot. Fenn. 33: 280. 1996. TIPO: *Amaranthus crispus* (Lesp. & Thévenau) J. M. Coult. & S. Watson [= *Euxolus crispus* Lesp. & Thévenau].

Goerziella Urb., Repert. Spec. Nov. Regni Veg. 20: 301. 1924. *Amaranthus* secc. *Goerziella* (Urb.) Mosyakin &

K. R. Robertson, Ann. Bot. Fenn. 33: 280. 1996. TIPO: *Amaranthus minimus* Standl. [= *Goerziella minima* (Standl.) Urb.].

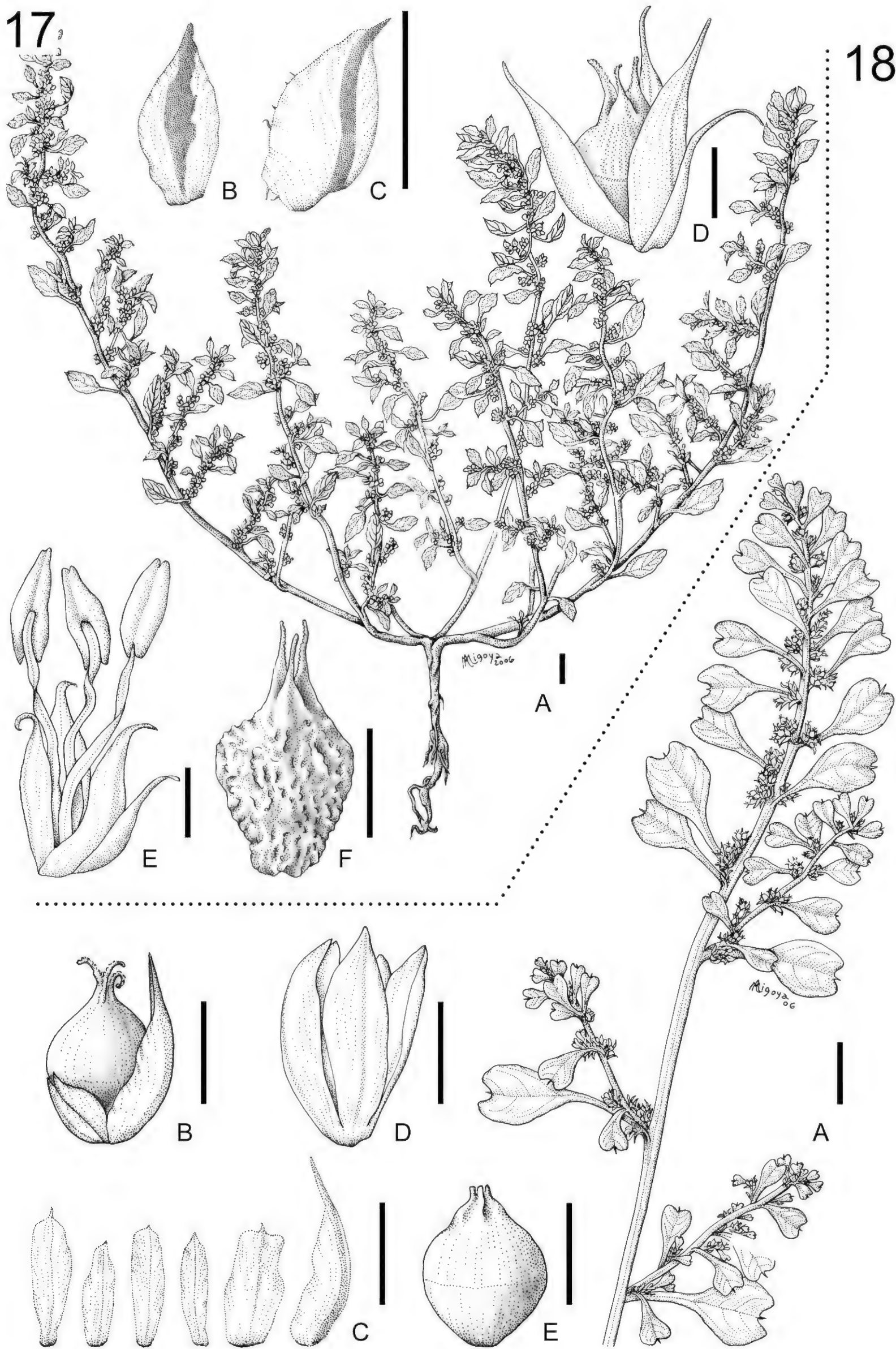
Hierbas anuales, monoicas; tallos principales por lo general postrados o ascendentes, otras veces erectos, rara vez carnosos (*Amaranthus californicus* y *A. pumilus*), glabros o glabrescentes, a veces pubescentes cuando jóvenes (*A. capensis* y *A. deflexus*) o también en plantas adultas (*A. crispus*), o solamente en la proximidad de las inflorescencias (*A. tricolor* y *A. viridis*). Hojas pecioladas, alternas, con lámina de forma variable, desde lineares a elípticas, atenuadas o cuneadas en la base, generalmente con un corto mucrón apical. Inflorescencias en glomérulos o breves inflorescencias espiciformes axilares, ocasionalmente terminales, pero entonces con glomérulos axilares desde la base de la planta; brácteas y bractéolas florales foliáceas, membranáceas, raramente espinescentes, las primeras sin una clara distinción entre la parte media y las laterales, las segundas con la vena media poco marcada y alas amplias y delgadas. Flores de ambos sexos sobre la misma inflorescencia (excepto en *A. minimus* donde las flores estaminadas y pistiladas se hallan separadas) siendo la primer flor de cada glomérulo estaminada, a la que se suman otras flores estaminadas entremezcladas entre las pistiladas. Flores estaminadas con (1) 3 a 5 sépalos y (1) 3 a 5 estambres. Flores pistiladas con (1) 3 a 5 sépalos y (2) 3 carpelos. Frutos indehiscentes, parcial o completamente dehiscentes, con dehiscencia transversal.

Etimología. Kunth le otorga el nombre en honor al médico Johann Christian Albers (1795-1857) quien se consagró al estudio de las plantas europeas.

Discusión. Existen varios nombres previos a *Amaranthus* subg. *Albersia* (Kunth) Gren. & Godr., pero todos ellos en rangos distintos del de subgénero. Según el Artículo 11.2. (McNeill et al., 2012) los nombres no tienen prioridad fuera del rango en el que están publicados, siendo el nombre *Amaranthus* subg. *Albersia* el primero en ser publicado en el rango de subgénero. Dumortier (1827) propone

Figura 17. *Amaranthus* L. subg. *Albersia* (Kunth) Gren. & Godr. —A. Planta de *A. crispus* (Lesp. & Thévenau) J. M. Coult. & S. Watson. —B. Bráctea foliácea de *A. viridis* L. —C. Bráctea membranácea de *A. deflexus* L. —D. Flor pistilada de *A. thunbergii* Moq. —E. Flor estaminada de *A. capensis* Thell. —F. Fruto indehiscente de *A. standleyanus* Covas. A, ilustrado de Daciuk 726 (LP); B, de Bayón 876 (LPAG); C, de Bayón 625 (LPAG); D, de Harbor s.n. (US-946741); E, de Probst 2833 (SI); F, de Ahumada & Castillón 4745 (SI). La barra de escala para A = 1 cm; para B-F = 1 mm.

Figura 18. *Amaranthus acutilobus* Uline & W. L. Bray. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A, ilustrado de Nee & Soule 33048 (MO); B-E, de Ventura 2209 (US). La barra de escala para A = 1 cm; para B-E = 1 mm.



Amaranthus secc. *Blitopsis* para aquellas especies que carecen de fruto pixidio y con bractéolas no espinosas. Rafinesque (1837: 41–42) publica varios nombres genéricos: *Dimeianthus* (sinónimo del nombre anterior *Bliton*), *Euxolus* (de frutos indehiscentes), *Amblogyna* (de flores pistiladas infundibuliformes) y *Pentrius* caracterizado como un género peculiar (“a peculiar genus”; este último no válidamente publicado al ser propuesto como nombre provisional, cf. Art. 36.1.b, McNeill et al., 2012). Moquin (1849) propuso *Amaranthus* secc. *Pyxidium* en la que incluyó a especies de *Amaranthus* subg. *Albersia* con frutos dehiscentes como *A. albus*, *A. graecizans* (pero usando erróneamente el nombre de *A. blitum*), *A. thunbergii* y *A. tricolor* (pero usando el nombre de *A. melancholicus* L.). Consideró como válidos a varios géneros de especies de flores monoicas que hoy se toman como sinónimos de *Amaranthus* subg. *Albersia*, a saber: *Amblogyna* (con una única especie, *Amaranthus polygonoides*), *Euxolus* (con *A. interruptus*), *Mengea* (con *A. californicus* y *A. peruvianus*), *Sarratia* (con *A. polygonoides*, *A. scariosus* y *A. urceolatus*), *Scleropus* Schrad. (con *A. crassipes*). En 1909, Beck crea *Euxolus* secc. *Pentamorion* basándose en los frutos indehiscentes y en las flores pistiladas con cinco sépalos espatulados.

CLAVE PARA DIFERENCIAR LAS ESPECIES (52) DE
AMARANTHUS SUBG. *ALBERSIA*

- 1. Frutos dehiscentes de tipo pixidio (a veces también indehiscentes en *A. schinzianus* y *A. sclerantoides*) 2
- 1'. Frutos indehiscentes (a veces dehiscentes o irregularmente dehiscentes en *A. schinzianus* y *A. sclerantoides*) 21
- 2(1). Sépalos de las flores pistiladas 1 a 3, a menudo sólo uno bien desarrollado mientras que los otros dos quedan reducidos a escamas o pueden faltar 7. *A. californicus* (Moq.) S. Watson
- 2'. Sépalos de las flores pistiladas 3 a 5, cuando son 3 todos están bien desarrollados 3
- 3(2'). Flores pistiladas con 3 sépalos 4
- 3'. Flores pistiladas con un número constante de 5 sépalos o con un número variable de (3)4 o 5 sépalos 10
- 4(3). Brácteas y bractéolas de las flores pistiladas subuladas, espinescentes, casi doblando en longitud a los sépalos 2. *A. albus* L.
- 4'. Brácteas y bractéolas de las flores pistiladas menores, iguales o excediendo apenas en longitud a los sépalos 5
- 5(4'). Sépalos menores que el fruto 18. *A. graecizans* L.
- 5'. Sépalos mayores que el fruto 6
- 6(5'). Brácteas, bractéolas florales y sépalos de las flores pistiladas con arista recta o curva 7
- 6'. Brácteas y bractéolas florales y sépalos de las flores pistiladas con el ápice no aristado ... 8

- 7(6). Sépalos con su porción más ancha en la mitad superior; plantas cultivadas con hojas de coloraciones a menudo vistosas .. 47. *A. tricolor* L.
- 7'. Sépalos con su porción más ancha en la mitad inferior; plantas silvestres con hojas verdes, carentes de coloraciones vistosas ... 45. *A. thunbergii* Moq.
- 8(6'). Sépalos de las flores pistiladas no estrechándose en un acumen 37. *A. rhombeus* R. Br.
- 8'. Sépalos de las flores pistiladas estrechándose en un acumen corto, de 0.10–0.50(–0.75) mm long, pero si supera esa longitud es reflejo y ganchudo 9
- 9(8'). Sépalos de las flores pistiladas lanceolados a espatulados, obtusos, subagudos o atenuados en un acumen uncinado de 0.10–0.25 mm long, generalmente 1 o 2 de ellos ensanchados en la mitad distal, zona que se presenta enteramente de color verde; anteras 1–2 mm long 8. *A. capensis* Thell.
- 9'. Sépalos de las flores pistiladas ovados a oblongos, agudos, estrechándose en un acumen que tiende a alejarse del centro de la flor, de 0.10–0.50(–0.75) mm long, no ensanchados en la mitad distal, zona que se presenta de tonalidad blancuzca con venas de color verde; anteras 0.5–1 mm long ... 16. *A. dinteri* Schinz
- 10(3'). Flores pistiladas con un número constante de 5 sépalos 11
- 10'. Flores pistiladas con número variable de (3)4 o 5 sépalos 16
- 11(10). Inflorescencias axilares en glomérulos, las que pueden agruparse apicalmente en inflorescencias hojosas 12
- 11'. Inflorescencias terminales espiciformes sin hojas, al menos en el extremo de las mismas .. 14
- 12(11). Pedúnculos florales y brácteas muy engrosados y endurecidos; base de los estilos muy ensanchada 41. *A. scleropoides* Uline & W. L. Bray
- 12'. Pedúnculos florales y brácteas no engrosados ni endurecidos; base de los estilos no ensanchada 13
- 13(12'). Tallos postrados o ascendentes; brácteas y bractéolas florales orbiculares, ovadas, elípticas o deltoides 20. *A. hunzikeri* N. Bayón
- 13'. Tallos ascendentes o erectos; brácteas y bractéolas lanceolado-ovadas 44. *A. tamaulipensis* J. Henrickson
- 14(11'). Brácteas y bractéolas varias veces más largas que los sépalos, 5–8 mm long 51. *A. viscidulus* Greene
- 14'. Brácteas y bractéolas a lo sumo un poco mayores que los sépalos, pero nunca llegando a doblarlos en longitud, menores a 2.5 mm long 15
- 15(14'). Brácteas y bractéolas lanceoladas u ovadas, menores que los sépalos ... 48. *A. undulatus* R. Br.
- 15'. Brácteas y bractéolas angustiovadas, lineares o lanceoladas, iguales o algo mayores que los sépalos 46. *A. torreyi* (A. Gray) S. Watson
- 16(10'). Inflorescencias predominantemente terminales, sin hojas; pueden presentarse también inflorescencias axilares .. 10. *A. clementii* Domin

16'.	Inflorescencias en glomérulos axilares que a veces pueden reunirse en el ápice dando origen a pseudoespigas generalmente con hojas 17	28(27).	Hojas con la lámina linear o linear-lanceolada 6. <i>A. brownii</i> Christoph. & Caum
17(16').	Flores pistiladas con sépalos obtusos en el ápice 18	28'.	Hojas con la lámina ovada o rómbica 50. <i>A. viridis</i> L.
17'.	Flores pistiladas con sépalos agudos en el ápice 19	29(27').	Pericarpio con costillas prominentes o débiles, longitudinales, rectas o infladas y onduladas 30
18(17).	Vena media de los sépalos de las flores pistiladas no ramificada 39. <i>A. schinzianus</i> Thell. (en parte)	29'.	Pericarpio sin costillas 32
18'.	Vena media de los sépalos de las flores pistiladas ramificada 39. <i>A. pedersenianus</i> N. Bayón & C. Peláez	30(29).	Inflorescencias en glomérulos axilares; costillas del fruto infladas y onduladas 28. <i>A. mitchellii</i> Benth.
19(17').	Hojas con la lámina linear, linear-obcordada, obcordada o cuneada, con el ápice dilatado 40. <i>A. sclerantoides</i> (Andersson) Andersson (en parte)	30'.	Inflorescencias en glomérulos axilares y también en espigas terminales; costillas del fruto poco elevadas y rectas 31
19'.	Hojas con la lámina de forma variada (lanceolada, obovada, oblongo-lanceolada, elíptica, espatulada, oblonga o casi linear) con el ápice no dilatado 20	31(30').	Hojas lineares, angostamente oblongas a angostamente ovadas; márgenes de los sépalos de las flores pistiladas con proyecciones a modo de dientes a cada lado 21. <i>A. induratus</i> C. A. Gardner ex J. Palmer & Mowatt
20(19').	Hojas adultas (0.3–)5–12 mm de ancho; flores pistiladas con (3)4 o 5 sépalos desiguales entre sí, con mucrón de 0.2 mm long 4. <i>A. blitoides</i> S. Watson	31'.	Hojas ovadas o elípticas; márgenes de los sépalos de las flores pistiladas sin proyecciones a modo de dientes a cada lado 9. <i>A. centralis</i> J. Palmer & Mowatt
20'.	Hojas adultas 1–10 mm de ancho; flores pistiladas con 4 o 5 sépalos similares entre sí, con un acumen conspicuo de 0.25–1 mm long 35. <i>A. praetermissus</i> Brenan	32(29').	Ejes de las inflorescencias engrosados y endurecidos; estilo dividido en dos ramas curvas que adoptan la forma de una lira .. 12. <i>A. crassipes</i> Schltdl.
21(1').	Flores pistiladas y estaminadas en inflorescencias separadas (en una misma planta): las masculinas apareadas, sobre pedúnculos largos, las femeninas solitarias o apareadas, sentadas en las axilas foliares 27. <i>A. minimus</i> Standl.	32'.	Ejes de las inflorescencias no engrosados ni endurecidos; estilo no en forma de lira 33
21'.	Flores pistiladas y estaminadas agrupadas en la misma inflorescencia 22	33(32').	Sépalos de la flor pistilada con su base engrosada, formada por un tejido esponjoso .. 34
22(21').	Flores pistiladas con 1 sépalo (raramente 2) .. 23	33'.	Sépalos de la flor pistilada con su base no engrosada (no formada por tejido esponjoso) .. 38
22'.	Flores pistiladas con más de 1 sépalo 24	34(33).	Flores con el cáliz expandido, de 3.5–5 mm diám en la porción distal ... 42. <i>A. squamulatus</i> (Andersson) B. L. Robinson
23(22).	Ejes de las cimas notablemente curvados y engrosados; hojas lineares con ápice bifurcado y pecíolo poco diferenciado 17. <i>A. furcatus</i> J. T. Howell	34'.	Flores con el cáliz expandido de 2.5 mm diám o menos en la porción distal 35
23'.	Ejes de las cimas no curvados ni engrosados; hojas espatuladas o suborbiculares, sin el ápice bifurcado, con pecíolo bien diferenciado de al menos 7 mm long 33. <i>A. peruvianus</i> (Schauer) Standl.	35(34').	Estambres 5 23. <i>A. kloosianus</i> Hunz.
24(22').	Flores pistiladas con 2 o 3 sépalos 25	35'.	Estambres 2–4 36
24'.	Flores pistiladas siempre con 3 sépalos, siempre con 5 sépalos o con un número variable entre 3 y 5 26	36(35').	Estambres 3 (raramente 2) 49. <i>A. urceolatus</i> Benth.
25(24).	Frutos superando ampliamente la longitud a los sépalos (sin llegar a duplicarlos en longitud), pericarpio liso 15. <i>A. deflexus</i> L.	36'.	Estambres 2 (a veces se suma un estaminodio) 37
25'.	Frutos apenas más largos que los sépalos, pericarpio rugoso 5. <i>A. blitum</i> L.	37(36').	Plantas poco ramificadas; hojas espatuladas 3. <i>A. anderssonii</i> J. T. Howell
26(24').	Flores pistiladas con un número constante de sépalos (en algunas especies 3, en otras 5) 27	37'.	Plantas muy ramificadas; hojas ovadas u obovado-rómbicas 34. <i>A. polygonoides</i> L.
26'.	Flores pistiladas con número variable de sépalos entre 3 y 5 (a veces 3 o 4, otras 4 o 5 o 3 a 5) 45	38(33').	Plantas crasas, con las hojas agrupadas en el extremo de los tallos 36. <i>A. pumilus</i> Raf.
27(26).	Flores pistiladas siempre con 3 sépalos 28	38'.	Plantas no crasas, con sus hojas no agrupadas en el extremo de los tallos 39
27'.	Flores pistiladas siempre con 5 sépalos 29	39(38').	Sépalos de las flores pistiladas ampliamente espatulados, con el limbo de 1.5–1.8 mm de ancho 14. <i>A. cuspidifolius</i> Domin
		39'.	Sépalos de las flores pistiladas de distintas formas (incluso espatulados), pero nunca ampliamente espatulados, con el limbo menor a 1.5 mm de ancho 40
		40(39').	Sépalos de la flor pistilada oblongo-obovados u oblongo-espatulados, adpresos al fruto, con su base de 0.3–0.5 mm de ancho no estrechada en una uña 52. <i>A. vulgatissimus</i> Speg.
		40'.	Sépalos de la flor pistilada nunca oblongos, pudiendo ser angostamente espatulados,

espatulados u obovados, reflejos, rectos o \pm adpresos al fruto, adelgazados en la base en una uña menor a 0.3 mm de ancho (en al menos dos de ellos) 41

41(40'). Hojas con la lámina ondulada 13. *A. crispus* (Lesp. & Thévenau) J. M. Coult. & S. Watson

41'. Hojas con la lámina no ondulada 42

42(41'). Inflorescencia exclusivamente en glomérulos axilares 43

42'. Inflorescencias tanto axilares como terminales 44

43(42). Flores pistiladas con sépalos 1.2–1.6(–2.3) mm long 11. *A. cochleitepalus* Domin

43'. Flores pistiladas con sépalos de 4–8 mm long 19. *A. grandiflorus* (J. M. Black) J. M. Black

44(42'). Pecíolo 1.8–5 cm; sépalos de las flores pistiladas espatulados de 1.5–2.8 mm long 43. *A. standleyanus* Covas

44'. Pecíolo 0.3–0.8 cm; sépalos de las flores pistiladas angostamente espatulados de 1.4–1.7 mm long 22. *A. interruptus* R. Br.

45(26'). Frutos superando ampliamente la longitud a los sépalos (sin llegar a duplicarlos) 26. *A. macrocarpus* Benth.

45'. Frutos menores, nunca mucho más largos que los sépalos 46

46(45'). Hojas muy conspicuamente emarginadas en el ápice, 2–13 mm de ancho 1. *A. acutilobus* Uline & W. L. Bray

46'. Hojas no emarginadas en el ápice (si son emarginadas angostas, de 1–5 mm de ancho) 47

47(46). Flores pistiladas con los sépalos soldados en la base 48

47'. Flores pistiladas con los sépalos libres 49

48(47). Pericarpio liso; flores pistiladas con 3 o 4 sépalos 24. *A. lombardoi* Hunz.

48'. Pericarpio rugoso; flores pistiladas con (4)5 sépalos 30. *A. obcordatus* (A. Gray) Standl.

49(47'). Hojas de lámina ovada 38. *A. rosenfurtii* Hunz.

49'. Hojas de lámina linear, linear-lanceolada u oblonga 50

50(49'). Lámina desde apenas hasta ampliamente dilatada apicalmente 40. *A. sclerantoides* (Andersson) Andersson (en parte)

50'. Lámina no dilatada apicalmente 51

51(50'). Pericarpio liso 25. *A. looseri* Suessen.

51'. Pericarpio rugoso 52

52(51'). Flores pistiladas con sépalos largamente mucronados (mucrón de 0.25–0.4 mm long) 32. *A. persimilis* Hunz.

52'. Sépalos de las flores pistiladas sin mucrón o a lo sumo con un mucrón muy breve 53

53(52'). Inflorescencias apicales no hojosas; brácteas y bractéolas florales de 1–1.5 mm long ... 29. *A. muricatus* (Moq.) Hieron.

53'. Inflorescencias apicales hojosas; brácteas y bractéolas florales de 0.6–0.75 mm long .. 39. *A. schinzianus* Thell. (en parte)

II. 1. *Amaranthus acutilobus* Uline & W. L. Bray, Bot. Gaz. 19: 320. 1894. *Euxolus emarginatus* A. Braun & C. D. Bouché, Index Sem. (Berlín) 4, 13. 1851, nom. illeg. TIPO: México. s. loc.,

1851, *A. Braun* s.n. (holotipo, B [†, 1943], lectotipo, designado por Bayón y Freire [2011: 175], MO-1740841!). Figura 18.

Hierbas anuales; tallos principales decumbentes, ascendentes o más raramente erectos, 15–35 cm, ramificados desde la base, de color verde, a veces con algunos tintes rosados. Hojas con pecíolo delgado de 3–15 mm, glabras, lámina romboide-ovada a espatulada u obcordada, ondulada, 5–20 \times 2–13 mm, atenuada a cuneada en la base, ápice emarginado, con los lóbulos agudos o redondeados y escotadura en forma de U o V, provista de mucrón. Inflorescencias axilares, en glomérulos de hasta 10 mm diám, agrupados hacia el ápice de los tallos; brácteas y bractéolas ovado-lanceoladas, 1.5–2(–3) mm, hasta el doble de la longitud de las flores pistiladas, igualando a las estaminadas, espinescentes, con la vena media prominente, de color verde, algunas veces reflejas. Flores de ambos sexos reunidas en una misma inflorescencia. Flores estaminadas con 4 o 5 sépalos elíptico-oblongos, 1.8–2.5 mm, agudos, desiguales, 4 o 5 estambres. Flores pistiladas con 4(5) sépalos oblongos u oblongo-lanceolados, 0.75–1.2 mm, desiguales, uno de ellos más largo; estigmas 3, delgados, 0.6 mm. Frutos indehiscentes, pericarpio liso y delgado; semillas de color castaño oscuro, 1–1.2 mm diám, semibrillantes, con poros pequeñísimos.

Distribución y ecología. *Amaranthus acutilobus* es nativa del Centro y Sur de México. Esta especie es adventicia en Europa, donde está presente en Alemania, Austria e Italia; fue encontrada una vez en Gran Bretaña (Standley, 1917). Se la encuentra en planicies áridas cultivadas con cereales (sobre todo maíz), o bien en tierras ocupadas por pastizales bajo pastoreo. Crece hasta los 2450 m. Florece entre julio y noviembre.

Discusión. Las hojas emarginadas de *Amaranthus acutilobus* recuerdan principalmente a las de *A. blitum* subsp. *emarginatus* y en menor medida a *A. viridis*. No obstante, el primero de los taxones presenta dos o tres sépalos y el segundo tres, no cuatro (o cinco) como *A. acutilobus*. Otras diferencias consisten en la longitud de las bractéolas y en la rugosidad que presentan los frutos: tanto en *A. blitum* subsp. *emarginatus* como en *A. viridis* las bractéolas son más breves que los sépalos y a lo sumo mucronadas (no más largas y espinescentes como ocurre en *A. acutilobus*) y los frutos son de superficie rugosa (no lisa como en *A. acutilobus*).

Ejemplares examinados. MÉXICO. México: Mpio. de Ajapusco, Jaltepec, *A. Ventura* 2209 (CTES, US). Puebla: Ca. de Puebla, Huejotzingo, *Arsène* 6121, 7104 (ambos en

US); 3 km E de San Nicolás Buenos Aires, *M. Nee & J. Soule 33048* (MO). **Veracruz:** Mpio. Perote, *M. Nee 32823* (MO).

II. 2. *Amaranthus albus* L., Syst. Nat., ed. 10, 2: 1268. 1759. *Galliardia albida* Bubani, Fl. Pyren. 1: 185. 1897, nom. inval. [*Galliardia* Bubani, nom. nud.]. TIPO: [Estados Unidos de América.] “Habitat [in Philadelphiae maritimis]”, *Herb. Linnaeus 1117.1* (lectotipo, LINN no visto, designado por Raus en Strid & Kit Tan [1997: 143], LINN 1117.1 no visto, imagen!). Figura 19.

Amaranthus graecizans L. var. *pubescens* Uline & W. L. Bray, Bot. Gaz. 19: 317. 1894. *Amaranthus pubescens* (Uline & W. L. Bray) Rydb., Bull. Torrey Bot. Club 39: 313. 1912. *Amaranthus albus* L. var. *pubescens* (Uline & W. L. Bray) Fernald, Rhodora 47: 140. 1945. TIPO: Estados Unidos de América. Nuevo México: Silver City, 16 jul. 1880, *E. L. Greene 185* (lectotipo, designado por Bayón y Freire [2011: 174], GH [código de barras] GH00036994!; isolectotipo, NY [cb] NY00324452!).

Hierba anual; tallos principales por lo general erectos, proximalmente ascendentes, 0.1–0.5(–1) m, fuertes, ramificados, glabros, o pubérulos en la porción superior, de color verde claro, plantas grandes, estepicursoras. Hojas con pecíolo de hasta 3.5 cm, glabras o pubescentes, lámina obovada a oblonga o espatulada, ondulada, 0.55–5(–7) × 0.2–1.6 cm, angostamente cuneada en la base, generalmente obtusa y a veces retusa en el ápice, de margen entero, con mucrón de 1 mm. Inflorescencias axilares, en glomérulos de 4–5 mm diám, esparcidos en los tallos, de color verde o verde-amarillento; brácteas y bractéolas linear-lanceoladas o aciculares, 2–4 mm, casi doblando en longitud a los sépalos, subuladas y espinescentes. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con 3(4) sépalos, 1.5–2 mm, subiguales, elípticos u obovados, 3 estambres. Flores pistiladas con 3 sépalos angostamente ovados a lineares, 0.8–1.5 mm, algo desiguales, espinuloso-apiculados, pálidos, membranáceos, con la vena media verdosa; estigmas 3, delgados, 0.4–0.7 mm. Frutos dehiscentes, iguales o más largos que los sépalos, urna lisa o poco rugosa, opérculo rugoso; semillas de color castaño-rojizo a negro, 1 mm diám, brillantes.

Distribución y ecología. *Amaranthus albus* es originaria de México y se halla naturalizada en América del Norte y del Sur, Eurasia, África y Australia. Prefiere lugares disturbados, con acumulación de desperdicios, costado de rutas (*Minshall 3985*, LP), cursos de agua, áreas arenosas o campos agrícolas. En algunos casos es considerada maleza

(Pedersen, 1994; Mosyakin & Robertson, 2003). Crece entre el nivel del mar y los 2200 m. En Argentina florece entre diciembre y mayo, mientras que en México y los Estados Unidos de América entre julio y octubre.

Nombres vulgares. Cardo ruso (*Burkart 3828*, SI); yuyo bola (de la Peña & Pensiero, 2004); tumbleweed amaranth, tumble pigweed, white amaranth (Mosyakin & Robertson, 2003).

Discusión. *Amaranthus albus* es una especie parecida a *A. californicus* por sus frutos dehiscentes y la morfología de sus flores pistiladas. Ambas especies presentan brácteas y bractéolas subuladas y espinescentes, casi doblando en longitud a los sépalos. No obstante, *A. californicus* posee plantas postradas (no erectas ni ascendentes), con uno a tres sépalos en las flores pistiladas, muy desiguales entre sí, a veces incluso reducidos a escamitas (no similares entre sí como en *A. albus*).

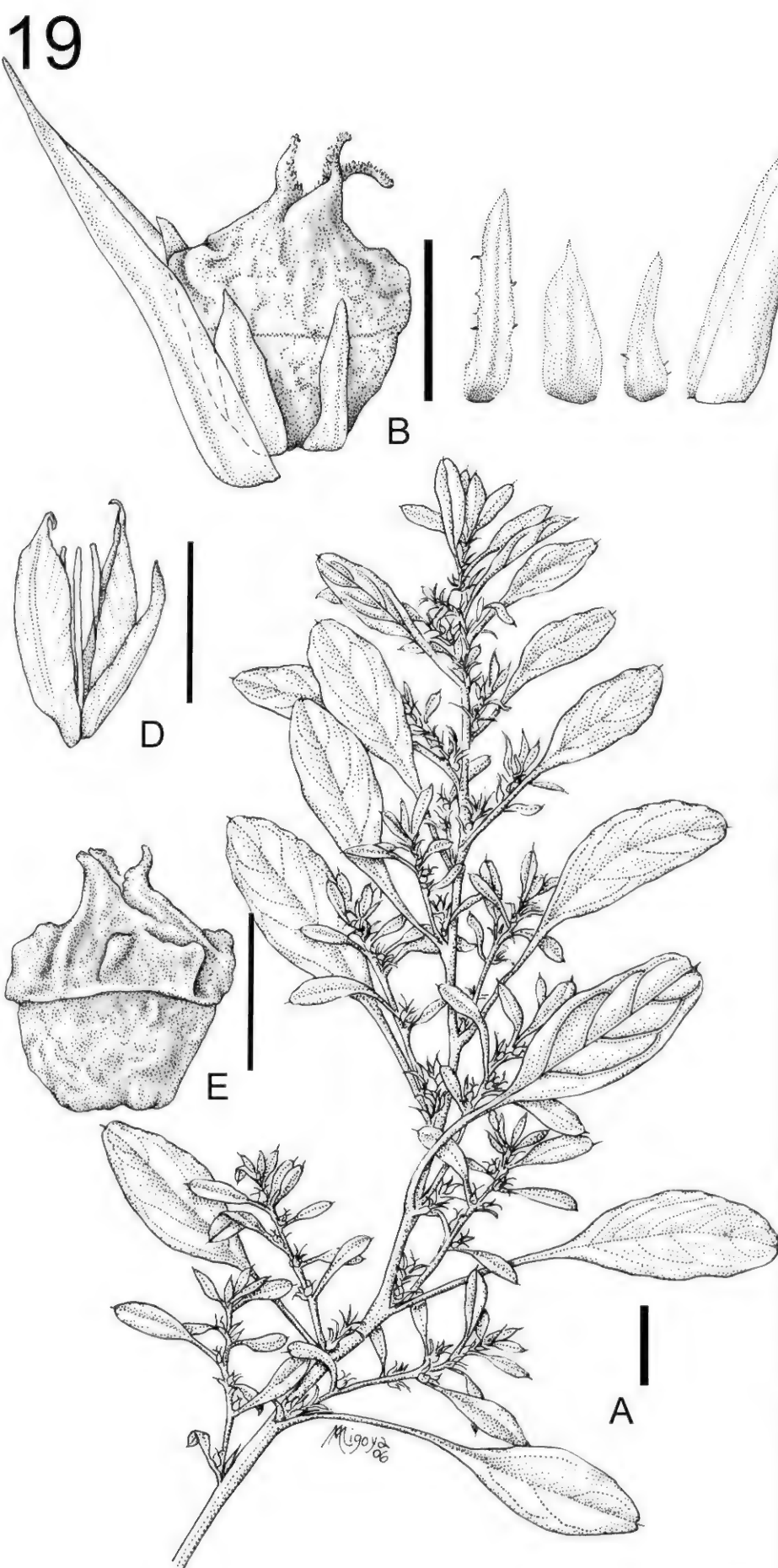
Ejemplares examinados. ARGENTINA. **Buenos Aires:** Pdo. Rivadavia, *A. Burkart 3828* (SI); Pdo. La Plata, La Plata, oct. 1940, *M. E. Marino s.n.* (LP). **Ciudad Autónoma de Buenos Aires:** Jardín Botánico de la Fac. de Agronomía, mar. 1932, *A. Burkart s.n.* (SI). **Córdoba:** Dep. Río Cuarto, *A. T. Hunziker & R. Subils 24804* (CORD). **La Pampa:** Dep. Utracán, Gral. Acha, Vivero Pampeano, *J. Williamson 574* (BAB); Dep. Maracó, Gral. Pico, 27 mar. 1944, *Williamson s.n.* (BAB). **Río Negro:** Dep. Bariloche, Parque Nac. Nahuel Huapi, Dest. Militar, *R. De Barba 306* (LIL). **San Luis:** Dep. Gral. Pedernera, Villa Mercedes, *D. L. Anderson 1076* (BAB); Est. INTA, *D. L. Anderson & J. E. Alliney 3046* (CORD); Ea. El Amanecer, 15 km N de Justo Daract, *D. L. Anderson et al. 3018* (CORD). URUGUAY. **Paysandú:** Meseta Artigas, *Rosengurt B-9326* (CTES).

IRAK. **Tarmiyah:** Baghdad, *R. Wheeler Haines W 15* [seeds, cult. at Kew K-4693] (SI). UZBEKISTÁN. Montes Meridionales, Tian-schan occidentalis, in ruderalis urbis Taschkent, *Linczewski & Vvedensky 422b* (BA-31/423); Montes Meridionales, Tian-schan occidentalis, in ruderalis urbis Taschkent, *P. Gomolitzky & A. Vvedensky 422* (BA-31/424).

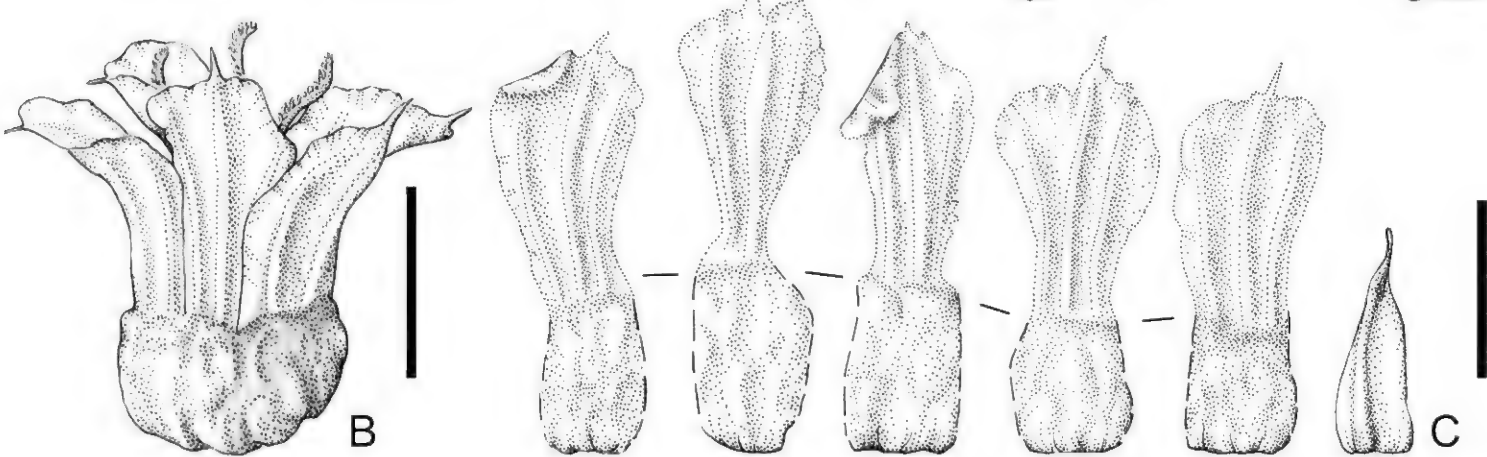
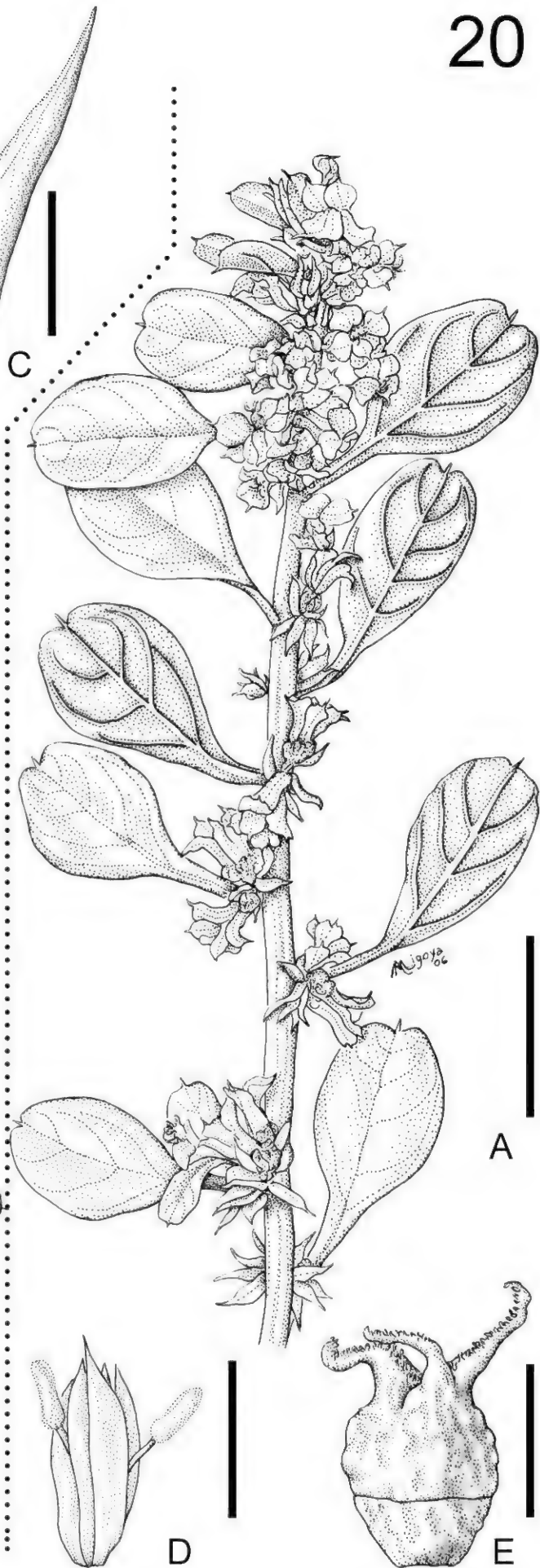
AUSTRIA. Lower Austria, Fischamend Market E Viena, *W. Till 136* (BA). ESPAÑA. **Cádiz:** Arcos de la Frontera, *T. M. Pedersen 14980* (CTES). FRANCIA. **Haut-Rhin:** Baumwolikompost in Issenheim, *T. M. Pedersen et al. 24* (CTES). GRECIA. **Creta:** Heraklion, *A. Hansen 1251* (CTES). HUNGRÍA. Syör, auf macktem land bei der Lambziegelfabrik, *S. Polgár 639* (SI); Syör, ait fabricam olei, *S. Polgár 739e* (SI); Syör ad fabricam olei Meller, *S. Polgár 2702* (SI). ITALIA. **Palermo:** Bagheria, *Todaro 405* (BAB). Palermo, s. coll. 28 (SI). REPÚBLICA CHECA. **Praga:** Troja, Bohemia centralis, oct. 1937, *M. Deyl s.n.* (BA). RUMANIA. **Oltenia:** Distr. Dolj, *D. & M. Cîrtu 920* (BAB); Distr. Bacăviensis, Bacău, *D. Mititelu et al. 407* (BAB). SUIZA. **Zúrich:** Zúrich, Eilgutbahnhof zwischen Geleisen, 30 ago. 1950, *H. Bühner s.n.* (CTES-160857).

CANADÁ. **Ontario:** Halton Co., Trafalgar Twp., Oakville Ont., *W. H. Minshall 3985* (LP). **Québec:** Rigaud, comté de Vaudreuil, *F. E. Roy 3969* (LP). ESTADOS UNIDOS DE AMÉRICA. **California:** Mendocino Co., entre Alder Springs

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y Macdonal, W. L. *Jepson 17663* (CTES). **Idaho:** N. Idaho, Coeur d'Alene Mtns., J. B. Leiberg 1549 (BAB). **Massachusetts:** Hampshire Co., N Maple St. near Rte. 9, Hadley, H. E. Ahles 89043 (BAB, LP). **Nevada:** Empire City, 1865, Torrey 457 (sintipo, *Amaranthus graecizans* var. *pubescens*, GH); San Francisco Mtns., sep. 1879, F. H. Knowlton 198 (sintipo, *A. graecizans* var. *pubescens*, GH). **North Carolina:** Buncombe Co., S. W. Leonard 2581 (CTES). **Nuevo México:** s. loc., 1847, A. Fendler 731 (sintipo, *A. graecizans* var. *pubescens*, GH); Zuni, jul. 1874, F. T. Rutawch s.n. (GH). **Washington, D.C.:** along RR track, 25 jul. 1893, F. L. J. Boettcher s.n. (BAB).

II. 3. *Amaranthus anderssonii* J. T. Howell, Proc. Calif. Acad. Sci., ser. 4, 21: 95. 1933, nom. reemplazo. Sin. reemplazado: *Scleropus urceolatus* Andersson, Vet. Akad. Handl. Stockh. 1853 [1855]: 162, non *Amaranthus urceolatus* Benth., Bot. Voy. Sulphur, 158. 1844. [1846]. TIPO: Ecuador. Galápagos: Isla Indefatigable [Isla Santa Cruz, vic. Conway Bay], mayo 1852, [N. J.] Andersson s.n. (holotipo, S S-R-5637 no visto, imagen!). Figura 20.

Amaranthus anderssonii J. T. Howell f. *erectus* J. T. Howell, Proc. Calif. Acad. Sci., ser. 4, 21(4): 96. 1933. TIPO: Ecuador. Galápagos: Isla Duncan, 7 jun. 1932, J. T. Howell 9837 (holotipo, CAS-203293 no visto, imagen!).

Hierba anual; tallos principales ascendentes, algunas veces erectos, 30 cm, poco ramificados, apenas pubescentes cerca de la inflorescencia. Hojas con pecíolo de 2–5 mm, no claramente diferenciado de la lámina, glabras, lámina espatulada, no ondulada, 5–10 × 4–6 mm, atenuada a cuneada en la base, hendida en el ápice, con un mucrón de 0.3–0.4 mm. Inflorescencias axilares en glomérulos de 5–8 mm diám; brácteas y bractéolas lanceoladas a ovado-lanceoladas, 1–1.6 mm, más cortas que los sépalos, membranáceas, con vena media prominente, ápice acuminado. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con 5 sépalos lanceolados, 1–1.5 mm, agudos o acuminados, 2 estambres (a veces puede hallarse un pequeño rudimento de un tercer estambre). Flores pistiladas con cáliz formado por 5 sépalos espatulados, 2–2.5 mm, engrosados y soldados en la base en un tramo de ± 1 mm, no permitiendo que se vea el ovario entre ellos, con la mitad superior solapada y refleja, expandida y obtusa en el ápice, algunas veces con

una muesca, mucrón 0.2 mm, notablemente 3-nervados, con la vena media de color verde, no ramificada, las laterales rectas y apenas divergentes; tubo del cáliz de 0.7–1 mm diám, mientras que distalmente el cáliz expandido en flores desarrolladas de 1.5–2 mm diám, más largo que el fruto; estigmas 3, ensanchados en la base, 0.5–0.7 mm. Frutos indehiscentes (rara vez con una leve tendencia a ser dehiscentes), rugosos en la mitad superior, la base encerrada dentro del tubo del cáliz; semillas de color castaño-rojizo oscuro a negro, 0.8–1 × 0.6 mm, brillantes.

Distribución. *Amaranthus anderssonii* es una especie endémica de las Islas Galápagos, presente en las Islas Española, Santa Cruz y Santiago (Eliasson, 1985).

Discusión. *Amaranthus anderssonii* es muy cercana a *A. polygonoides*, *A. urceolatus* y *A. squamulatus*. *Amaranthus polygonoides* se diferencia porque presenta plantas más ramificadas y hojas ovadas, no espatuladas. Las diferencias con la segunda especie son por un lado, que *A. urceolatus* tiene tres estambres y los sépalos de las flores pistiladas están unidos en la base a lo largo de 0.5 mm, mientras que *A. anderssonii* posee dos estambres y la unión llega a 1 mm, sumándose el hecho que en *A. anderssonii* los sépalos de las flores pistiladas, en la parte media no permiten ver el ovario, lo que sí ocurre en *A. urceolatus*. Por otro lado, *A. squamulatus* tiene brácteas y bractéolas más largas (1.5–3.5 mm) y el cáliz de las flores pistiladas es amplio en la porción distal (3.5–5 mm diám), mientras que *A. anderssonii* tiene brácteas y bractéolas más cortas (1–1.6 mm) y el diámetro distal de la flor no supera los 2 mm. Además la base de los sépalos sobre los frutos maduros de *A. anderssonii* es de menor consistencia, esto es más esponjosa que en *A. squamulatus* y *A. urceolatus*.

Al trasladar Howell *Scleropus urceolatus* al género *Amaranthus* en 1933, utiliza el epíteto específico *anderssonii* pues el nombre *A. urceolatus* estaba asignado a una especie descrita por Benthham en 1844.

Según Howell (1933), *Amaranthus anderssonii* f. *erectus* presenta plantas de porte erecto y el cáliz algo más largo, de 2.5 mm. Ambos caracteres tienen poca relevancia como para justificar una nueva forma.

Figura 19. *Amaranthus albus* L. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A, ilustrado de Ahles 89043 (LP); B–E, de Anderson 1076 (BAB). La barra de escala para A = 1 cm; para B–E = 1 mm.

Figura 20. *Amaranthus anderssonii* J. T. Howell. —A. Hábito fértil. —B. Flor pistilada. —C. Bráctea y sépalos de la flor pistilada. —D. Flor estaminada. —E. Fruto. A–E, ilustrado de Howell 9696 (US). La barra de escala para A = 5 mm; para B–E = 1 mm.

Ejemplares examinados. ECUADOR. **Galápagos:** Isla James [Isla Santiago], Bahía James, *J. T. Howell* 9696 (US); Isla Hood [Isla Española], Punta Suárez, *H. van der Werff* 2055 (K).

II. 4. *Amaranthus blitoides* S. Watson, Proc. Amer. Acad. Arts 12: 273. 1877. *Galliardia blitoides* (S. Watson) Nieuwl., Amer. Midl. Naturalist 3: 278. 1914, comb. inval. [*Galliardia* Bubani, nom. nud.]. TIPO: Estados Unidos de América. Iowa: Ames, 1881, *C. E. Bessey s.n.* (lectotipo, designado por Fernald [1945: 139], GH [código de barras] GH00036983!). Figura 21.

Amaranthus blitoides S. Watson var. *crassius* Jeps., Fl. Calif. 1: 449. 1914. TIPO: Estados Unidos de América. Nevada: Reno, 26 ago. 1896, *W. L. Jepson s.n.* (holotipo, JEPS-3480 no visto, imagen!).

Amaranthus blitoides S. Watson var. *densifolius* Uline & W. L. Bray, Bot. Gaz. 19: 315. 1894. TIPO: Estados Unidos de América. Arizona, Hackberry, 18 sep. 1883, *Rusby 804* (lectotipo, designado por Bayón y Freire [2011: 173], NY [código de barras] NY00951459!, isoelectipos, [cb] NY951458!, MICH [cb] MICH1207149, MICH no visto, imagen!, US [cb] US00106234, US no visto, imagen!).

Amaranthus blitoides S. Watson var. *reverchonii* Uline & W. L. Bray, Bot. Gaz. 19(8): 315. 1894. TIPO: Estados Unidos de América. Texas: Dallas, oct. 1881, *J. Reverchon 824* (holotipo, US [código de barras] US00106236 no visto, imagen!).

Hierba anual; tallos principales ascendentes, raramente suberectos, 20–60 cm, ramificados, glabros. Hojas con pecíolo de 3–25 mm, glabras, lámina de forma variable: lanceolada, oblongo-lanceolada, obovada, elíptica o espatulada, no ondulada, 0.7–4 × (0.3–)0.5–1.2 cm, atenuada a cuneada en la base, obtusa en el ápice, mucronulada. Inflorescencias axilares, en glomérulos de 0.4–0.6 cm diám, a veces agrupados en el ápice de los tallos, simulando una inflorescencia terminal foliosa, de color verde; brácteas y bractéolas angostamente oblongas a lanceoladas, 1.5–2 mm, más cortas, de la misma longitud, o apenas excediendo la longitud de los sépalos, foliáceas, vena media ancha, acuminadas o aristadas. Flores de ambos sexos en una misma inflorescencia. Flores estaminadas con 3(4) sépalos ovado-acuminados, 1.3–2 mm, 3 estambres. Flores

pistiladas con (3)4 o 5 sépalos, angostamente oblongos, obovados u ovados, 1–2.5(–4) mm, agudos, usualmente desiguales, el mayor 1.2 a 1.5 veces más largo que la bractéola, con la vena media ramificada, mucrón 0.2 mm; estigmas tres, 0.25–0.5 mm. Frutos dehiscentes, casi tan largos como los sépalos, con el pericarpio liso o con el opérculo verrugoso; semillas de color negro, 1.3–1.8 mm diám, opacas.

Distribución y ecología. *Amaranthus blitoides* es originaria del centro y este de los Estados Unidos de América. En el presente se ha naturalizado en áreas templadas del norte de África, América del Norte y del Sur y Asia occidental. Se la puede hallar al costado de rutas, vías de ferrocarril, márgenes de cursos hídricos, campos de pastoreo, a veces en suelos arenosos (tipo, *Bessey s.n.*, GH) o como planta ruderal (*Boyd 6415*, BA). Crece entre el nivel del mar y los 2200 m (Pedersen, 1984; Mosyakin & Robertson, 2003). En la Argentina florece en noviembre, mientras que en el hemisferio norte entre julio y septiembre.

Nombres vulgares. Matweed, matweed amaranth, prostrate amaranth, prostrate pigweed (Mosyakin & Robertson, 2003).

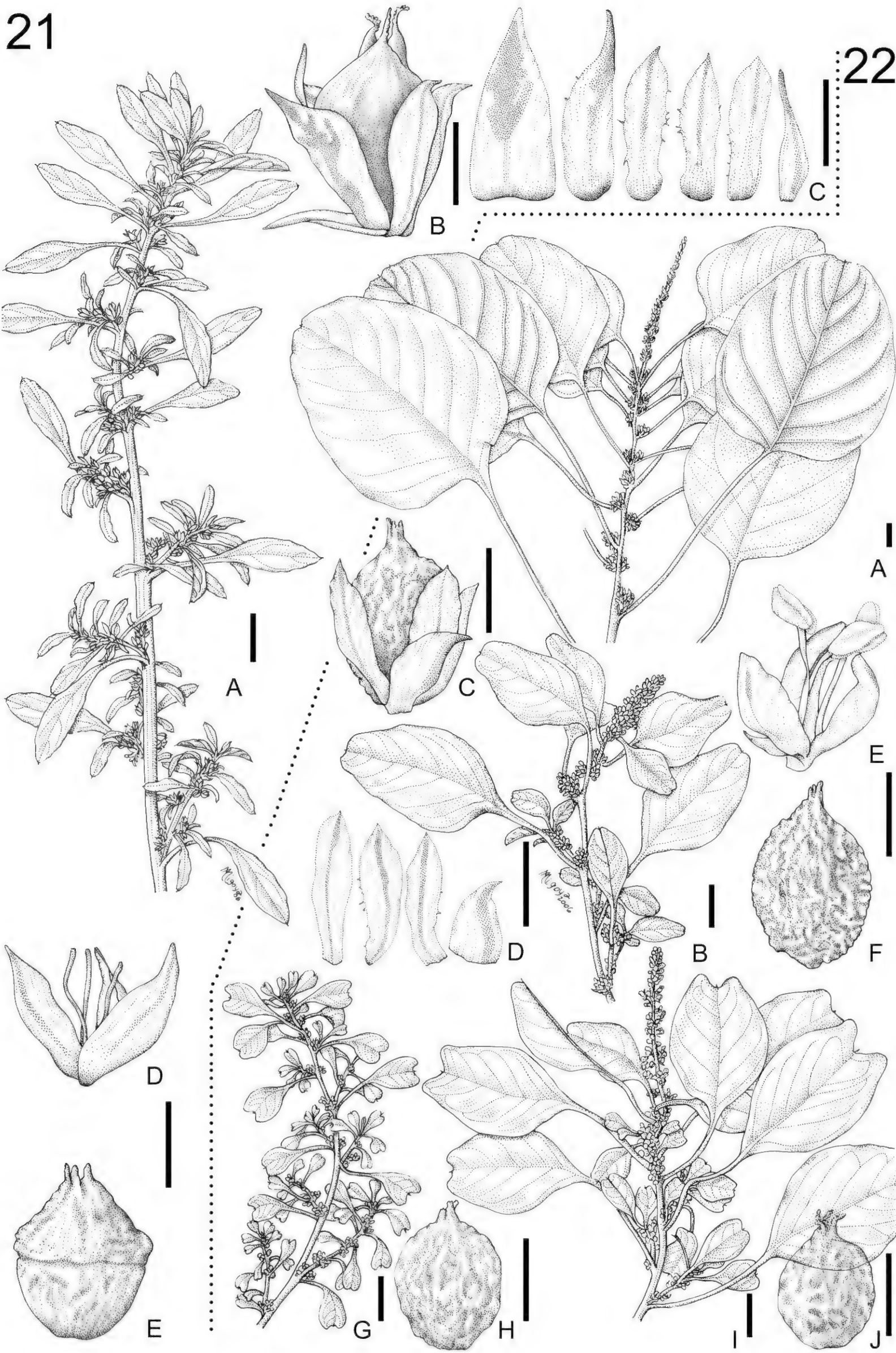
Discusión. *Amaranthus blitoides* se puede confundir con *A. graecizans* por el parecido de sus hojas. No obstante ello, *A. graecizans* presenta invariablemente flores pistiladas con tres sépalos mucronados o aristados (arista de hasta 0.75 mm), mientras que *A. blitoides* tiene flores pistiladas con (tres o cuatro) cinco sépalos mucronados (mucrón 0.2 mm). Presenta a su vez semejanza con *A. clementii* (Australia) y *A. praetermissus* (Sudáfrica). Las tres se parecen por sus hojas delgadas, sus inflorescencias en glomérulos axilares y sus frutos dehiscentes; aunque *A. clementii* tiene los sépalos de las flores pistiladas obtusos a emarginados, mientras que las otras dos especies los tienen agudos. *Amaranthus blitoides* tiene los sépalos de las flores pistiladas desiguales entre sí, con un mucrón de 0.2 mm, mientras que *A. praetermissus*, tiene los sépalos subiguales, con un acumen conspicuo de 0.25–1 mm.

Figura 21. *Amaranthus blitoides* S. Watson. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A–E, ilustrado de *Gonzalo 6891* (SI). La barra de escala para A = 1 cm; para B–E = 1 mm.

Figura 22. *Amaranthus blitum* L. subsp. *oleraceus* (L.) Costea. —A. Hábito fértil. *Amaranthus blitum* subsp. *blitum*. —B. Hábito fértil. —C. Flor pistilada. —D. Sépalos y bráctea de la flor pistilada. —E. Flor estaminada. —F. Fruto. *Amaranthus blitum* subsp. *emarginatus* (Salz. ex Moq.) Carretero, Muñoz Garmendia & Pedrol. —G. Hábito fértil. —H. Fruto. *Amaranthus blitum* subsp. *pseudogracilis* (Thell.) N. Bayón. —I. Hábito fértil. —J. Fruto. A, ilustrado de *Herb. Linnaeus 1117.13* (LINN); B–F, de *Legendre 3895* (LP); G–H, de *Lanfranchi 522* (LP); I–J, de *Bayón 626* (LPAG). Las barras de escala para A, B, G, I = 1 cm; para C–H, J = 1 mm.

21

22



Dentro de esta especie se ha reconocido la existencia de cuatro variedades: *Amaranthus blitoides* var. *crassius* Jeps., *A. blitoides* var. *densifolius* Uline & W. L. Bray, *A. blitoides* var. *halophilus* Aellen y *A. blitoides* var. *reverchonii* Uline & W. L. Bray. Uline y Bray (1894b) proponen las variedades *A. blitoides* var. *densifolius* y *A. blitoides* var. *reverchonii*, en base a los sintipos *H. H. Rusby 804* y *E. L. Greene 614* para la primera y el tipo *Reverchon 824* para la segunda. Caracterizan a *A. blitoides* var. *densifolius* por las hojas agrupadas en el extremo de los tallos, de 1–2 cm y los tallos delgados, y a *A. blitoides* var. *reverchonii* por sus hojas delgadas y no agrupadas, con el opérculo del pixidio de color marrón rojizo. El análisis de dos ejemplares de *H. H. Rusby 804* (NY), y de las imágenes de dos duplicados, uno de un ejemplar depositado en MICH y otro de un ejemplar de US, y de *Reverchon 824* depositado en US, confirman los caracteres mencionados por Uline y Bray, pero los cuales son parte de la variabilidad observada dentro de *A. blitoides*. Para Mosyakin y Robertson (2003) se trataría de formas ecológicas o variantes morfológicas carentes de significancia taxonómica. Jepson (1914) describe *A. blitoides* var. *crassius* sobre la base del ejemplar *W. L. Jepson s.n.* (JEPS-3480), por poseer como caracteres distintivos sus ramitas algo más gruesas, blancuzcas y ascendentes. Por su lado Aellen (1972) describe *A. blitoides* var. *halophilus*, basándose en el ejemplar *Behboudi & Aellen 2067* (G-00098623), con sépalos de consistencia más gruesa, coriácea, con la nervadura media muy engrosada y el ápice curvado hacia afuera. Del estudio de las fotografías recibidas de los materiales tipo, se desprende que los caracteres vegetativos propios de *A. blitoides* var. *crassius* no permitirían distinguirla de *A. blitoides*. Por el contrario, los rasgos diferenciales de *A. blitoides* var. *halophilus* son más relevantes y al parecer sería la única que merecería su reconocimiento como variedad.

Ejemplares examinados. ARGENTINA. **La Pampa:** Dep. Caleu Caleu, Río Colorado, *C. A. O'Donell 1626* (CTES-206083). **Río Negro:** Dep. Pichi Mahuida, *C. A. O'Donell 1723* (CTES).

UZBEKISTÁN. Montes meridionales Tian Schan occidental, Toskent, *P. Gomolitzky & A. Vvedensky 424* (BA).

MÉXICO. **Coahuila:** 5 mi. al W de El Oro, camino a Guimbalte, *S. S. White 1999* (SI).

BULGARIA. **Varna:** Beloslav, 5 sep. 1953, *N. Vihodzevsky s.n.* (SI). ESPAÑA. **Alicante:** *A. Schinini 31075* (CTES). **Cádiz:** Arcos de la Frontera, *T. M. Pedersen 14925* (CTES); Puerto de Cádiz, *T. M. Pedersen 14954* (CTES). **Cataluña:** Barcelona, Manlleu, *Gonzalo 5099, 6891* (ambos en SI); Barcelona, à Can Tunis, *F. Sennen 4214* (SI). EUROPA CENTRAL. Sin país det., *R. Scheuermann 2832 b* (SI). RUMANIA. **Moldavia:** Bacău, *D. Mititelu et al. 307* (BAB).

ESTADOS UNIDOS DE AMÉRICA. **California:** Riverside Co., Aguanga Valley, *S. Boyd 6436* (BA); Riverside Co., Temescal Canyon, W base of Gavilan Hills, *S. Boyd 6415* (BA).

II. 5. *Amaranthus blitum* L., Sp. Pl. 990. 1753.
Albersia blitum (L.) Kunth, Fl. Berol. 2: 144. 1838. *Euxolus blitum* (L.) Gren., Mém. Soc. Émul. Doubs. Ser. 3, 10: 652. 1869. TIPO: “Habitat in Europa temperiore”, *Herb. Linnaeus 1117.14* (lectotipo, designado por Fillias et al. [1980: 150], LINN 1117.14 no visto, imagen!). Figura 22.

Hierba anual o perenne de corta vida; tallos postrados, ascendentes o erectos, 10–50(–90) cm, simples o ramificados, glabros. Hojas con pecíolo de hasta 10 cm, glabras, lámina ovada a ovado-elíptica, no ondulada, 0.5–10 × 0.5–4.5 cm, redondeada o ampliamente cuneada en la base, emarginada hasta bilobada en el ápice, pocas veces redondeada, mucronulada. Inflorescencias axilares y terminales, las primeras en glomérulos de hasta 1 cm diám, a veces exclusivamente en esta forma, las segundas en espigas o más raro en panojas, de 0.5–8 × 0.4–0.8 cm, usualmente delgadas, delicadas, a veces sin hojas en la parte distal; brácteas y bractéolas ovado-deltoides a lanceoladas, 0.75–1 mm, más cortas o rara vez casi iguales a los sépalos, membranáceas, con la vena media de color verde ramificada o no, excurrente en un mucrón, que a veces puede faltar. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con 3 sépalos, ovados, agudos u obtusos, membranáceos con la vena media de color verde, 0.75–1.1 mm. Flores pistiladas con 2 o 3 sépalos, oblongos a espatulados, 1–1.5 mm, agudos a obtusos, con la vena media de color verde en la mitad superior; estigmas 2 o 3, cortos, 0.2–0.4 mm. Frutos indehiscentes, más largos que el cáliz, 1.2–2.6(–3) mm, rugosos; semillas de color castaño oscuro a negro, 0.8–1.8 mm diám, brillantes en el área central, y con el área marginal con escultura evidente o inconspicua.

Discusión. *Amaranthus blitum* es cercana por su aspecto a *A. viridis*, de la que se distingue por tener hojas marcadamente emarginadas y flores pistiladas con dos o tres sépalos, mientras que las hojas de *A. viridis* pueden ser sólo algo emarginadas y las flores pistiladas tienen sépalos en número de tres. Las hojas escotadas de *A. acutilobus* también recuerdan a las de *A. blitum* (sobre todo a *A. blitum* subsp. *emarginatus*). Sin embargo, *A. acutilobus* tiene flores pistiladas con cuatro sépalos (no dos o tres), brácteas y bractéolas el doble de la longitud de los sépalos y espinescentes (no más cortas y a lo sumo mucronadas) y frutos de pericarpio liso (no rugoso).

En el presente tratamiento se considera como válido el epíteto específico *blitum* para *Amaranthus blitum*. Existe un segundo nombre en disputa que es *A. lividus*. Tanto *A. blitum* como *A. lividus* aparecen en la primer edición del *Species Plantarum* (Linneo, 1753: 990). Con el último de estos nombres Linneo se refirió, en esta y otras obras, a la forma erecta, de grandes hojas, que era cultivada y que consideró como una especie distinta. Más tarde, el propio Linneo (1763: 1403) le otorga la nueva denominación específica de *A. oleraceus* L. Como bien establecen Fillias et al. (1980), dado que estas tres denominaciones corresponden a una misma especie, se le debe aplicar el nombre según el principio de prioridad. Según lo antedicho resulta que existen dos posibilidades de nombres legítimos, por lo que la primer elección posterior que sea efectivamente publicada según los Art. 29–31 (McNeill et al., 2012) establece la prioridad en el nombre elegido sobre los nombres que son competidores como se establece en el Art. 11.5 (McNeill et al., 2012). Hooker (1885) decide usar el nombre de la forma no cultivada (*A. blitum*) para referirse a la especie en su conjunto. Después Thellung (1919a: 320–321, e.g., *A. lividus* proles *polygonoides* (Moq.) Thell.) elige el epíteto *lividus* para designar a la especie, siendo muchos los autores que siguieron su criterio. Por lo tanto, para Fillias et al. la planta silvestre retiene el nombre de *A. blitum* L., siendo la subsp. *blitum* tipificada con el ejemplar de la derecha (no el de la izquierda, que pertenece a *A. graecizans* L.) de la hoja *Herb. Linnaeus 1117.14* del herbario LINN (aquí Fillias et al. [1980] agregan un error al controvertido caso, al mencionar como tipo al ejemplar *Herb. Linnaeus 1117.4* [no *Herb. Linnaeus 1117.14*], que en rigor es el lectotipo de *A. melancholicus*, el que se repite en la respuesta de Brenan y Townsend [1980] y otros trabajos posteriores).

Oponiéndose a lo expresado en el párrafo anterior, Brenan y Townsend (1980) sostienen que el nombre *Amarantus blitum* ha constituido una prolongada fuente de confusión y que por lo tanto debería ser incluido en la lista de *nomina rejicenda*, basándose en su errónea aplicación a *A. lividus* (según ellos) y a *A. graecizans*. Explican que entre los muchos autores que aplicaron erróneamente el nombre *A. blitum*, refiriéndose en rigor de verdad a *A. graecizans* está nada menos que Moquin, cuya obra constituyó una de las principales fuentes para el estudio del género durante muchos años. Para ellos, en este uso equivocado que hace Moquin radica el inicio de toda la confusión. Moquin (1849: 273) trata el nombre de *Euxolus lividus* Moq. [= *A. lividus* L.]. Este error se repite una y otra vez en gran cantidad de

floras en que se usa el epíteto *lividus*. Finalmente, Brenan y Townsend (1980) expresan que el nombre ha adquirido una estabilidad tal que sería irresponsable y carente de fundamento el volver al uso de *A. blitum*.

CLAVE PARA LA DIFERENCIACIÓN DE LAS SUBESPECIES DE *AMARANTHUS BLITUM*

1. Frutos de 1.8–2.6(–3) mm; semilla de 1.1–1.8 mm diám 2
- 1'. Frutos de 1.2–1.8 mm; semillas de 0.8–1.1 mm diám 3
- 2(1). Bractéolas con la vena media no ramificada; semillas con escultura evidente
..... *A. blitum* L. subsp. *blitum*
- 2'. Bractéolas con la vena media ramificada; semillas con escultura inconspicua
..... *A. blitum* L. subsp. *oleraceus* (L.) Costea
- 3(1'). Plantas postradas, hojas (0.75–)1–2(–3.5) cm long; inflorescencias enteramente formadas por cimas axilares (inflorescencias terminales reducidas o ausentes) *A. blitum* L. subsp. *emarginatus* (Uline & W. L. Bray)
Carretero, Muñoz Garmendia & Pedrol
- 3'. Plantas ascendentes, más vigorosas con hojas de 2–4(–6) cm long; inflorescencias principalmente de disposición terminal, larga, delgada y flexuosa
... *A. blitum* subsp. *pseudogracilis* (Thell.) N. Bayón

II. 5a. *Amaranthus blitum* L. subsp. *blitum*.

Amaranthus ascendens Loisel., Not. Fl. France: 141. 1810. *Amaranthus blitum* L. var. *ascendens* (Loisel.) DC., Cat. Pl. Horti Monsp. 4. 1813. *Euxolus viridis* var. *ascendens* (Loisel.) Moq. in de Candolle, Prodr. 13(2): 274. 1849. *Amaranthus lividus* [sin rango] *ascendens* (Loisel.) Thell., Syn. Mitteleur. Fl. 5(Abth. 1): 321–322. 1919, como “proles *ascendens*”. *Amaranthus lividus* L. var. *ascendens* (Loisel.) Hayw. & Druce, Advent. Fl. Tweedside 177. 1919. *Amaranthus lividus* L. subsp. *ascendens* (Loisel.) Heukels, Geill. Schoolfl. Nederl. ed. 11: 169. 1934. *Euxolus ascendens* (Loisel.) H. Hara, J. Jap. Bot. 14(5): 335–336. 1938. TIPO: tab. [s.n.] “*Blitum pulchrum rectum magnum rubrum*” en J. Bauhin & Cherler, Historia plantarum universalis ..., tomus II: 966. 1651 (lectotipo, designado por Townsend [1985: 35]). EPITipo: Francia. Córcega: entre Pte. D'Abatesco y Mignattaja südl. Von Ghisonaccia, 10 ago. 1933, *P. Aellen* 1960 (epitipo, aquí designado, LP-000281!).

Amaranthus blitum subsp. *blitum* posee brácteas y bractéolas con la nervadura central no ramificada, frutos de poco más de 2 mm, lisos cuando jóvenes y rugosos a la madurez y semillas de alrededor de 1.1–1.2 mm de diámetro, con escultura evidente en la zona marginal.

Distribución y ecología. *Amaranthus blitum* subsp. *blitum* es probablemente originaria de Europa (Mediterráneo); se la encuentra también en América (sobre todo en América Central y del Sur), norte de

África y Eurasia (Carretero, 1990; Costea et al., 2001c; Mosyakin & Robertson, 2003). Puede constituirse en maleza común en cultivos bajo riego y en sitios donde se arrojan desperdicios. Crece entre el nivel del mar y los 1000 m. En Europa florece entre julio y septiembre.

Nombres vulgares. Purple amaranth, livid amaranth (Mosyakin & Robertson, 2003).

Usos. Esta especie fue cultivada como hortaliza en Asia, África e islas del Pacífico, hasta que posteriormente fuera reemplazada por la espinaca (*Spinacia oleracea* L., *Amaranthaceae*).

Discusión. Loiseleur-Deslongchamps (1810: 141) en la diagnosis original de *Amaranthus ascendens* cita lo siguiente: “J. Bauh., Hist. 2, p. 967. Blitum albus majus. Tournf., Inst. 507, et Herb. Sic”. La obra de Bauhin cuenta con una ilustración, no así la de Tournefort. Con respecto a ella Loiseleur-Deslongchamps agrega: “La figure du Blitum pulchrum rectum magnum rubrum, J. Bauh., Hist. 966, la représente assez bien”. Dicha ilustración (Bauhin & Cherler, 1651: 966) constituye en consecuencia el holotipo de la especie y en ella se pueden observar claramente las hojas anchamente ovadas con el ápice emarginado y algunas inflorescencias. Sin embargo, en el detalle de la flor no se pueden apreciar las características de la bráctea floral ni la de los sépalos. Por esta razón, al considerar que esta ilustración es un tanto ambigua y que no puede ser identificada críticamente para el reconocimiento del nombre, se designa como epitipo al ejemplar *Aellen 1960* (LP) (Art. 9.7, McNeill et al., 2012).

Ejemplares examinados. FRANCIA. **Haute-Marne:** Perthes, Décombres, jardins, *C. Legendre 3895* (SI). SUECIA. **Estocolmo:** Estocolmo, *H. Agnér s.n.* (LIL). **Södermanland:** Paroecia Husby-Oppunda, Tärnö, *E. Asplund 722* (LIL). **Uppsala:** Uppsala, Linnéiska Trädgården, sep. 1995, *N. Pedersen s.n.* (CTES). SUIZA. **Tisino:** Malvaglia, Valle Leventina, *T. M. Pedersen 7944* (CTES, LP). Zürich, Gartenland an der Schmelzbergstrasse, *W. Kech 49/506* (CTES).

II. 5b. *Amaranthus blitum* L. subsp. *emarginatus* (Uline & W. L. Bray) Carretero, Muñoz Garmendia & Pedrol, *Anales Jard. Bot. Madrid* 44(2): 599. 1987. Basónimo: *Amaranthus emarginatus* Uline & W. L. Bray, *Bot. Gaz.* 19: 319. 1894, nom. reemplazo. Sin. reemplazado: *Euxolus viridis* (L.) Moq. var. *polygonoides* Moq. in de Candolle, *Prodr.* 13(2): 274. 1849. *Amaranthus ascendens* Loisel. var. *polygonoides* (Moq.) Thell., *Fl. Adv. Montpellier*: 215. 1912. *Amaranthus lividus* L. [sin rango] *polygonoides* (Moq.) Thell., *Syn. Mitteleur. Fl.* 5 (Abth. 1):

320. 1919, como “proles *polygonoides*”. *Amaranthus lividus* L. subsp. *polygonoides* (Moq.) Thell. ex Probst, *Wolladvenfl. Mitteleur.* 74. 1949. *Amaranthus ascendens* Loisel. subsp. *polygonoides* (Moq.) Thell. ex Priszter, *Agrártud. Egyet. Kert- Szőlőgazdaságtud. Karának Évk.* 2: 221. 1953. *Amaranthus blitum* L. var. *emarginatus* (Uline & W. L. Bray) Lambinon, *Bull. Soc. Échange Pl. Vasc. Eur. Occid. Médit.* 24: 55. 1993. *Amaranthus blitum* L. subsp. *polygonoides* (Zoll. ex Moq.) Carretero, *Anales Jard. Bot. Madrid* 41: 276. 1985, nom. illeg., non *A. blitum* var. *polygonoides* Moq. in de Candolle. 1849. TIPO: Indonesia. Java: “Sine loc., 21 Oct. 1843, *H. Zollinger 1646*” (lectotipo, designado por Hügin [1987: 461, primer paso], P; lectotipo, aquí designado [segundo paso], P [código de barras] P00572007 no visto, imagen!; isolectotipos, P [cb] P00572006 no visto, imagen!, G [cb] G00098622 no visto, imagen!, G-DC [cb] G-DC00138473 no visto, imagen!, STR no visto).

Los tallos de *Amaranthus blitum* subsp. *emarginatus* son postrados o ascendentes, mientras que sus hojas son profundamente emarginadas o bilobadas en el ápice. Las inflorescencias están enteramente formadas por cimas axilares (inflorescencias terminales reducidas o ausentes), los frutos son menores a 1.8 mm y las semillas tienen menos de 0.8–1.1 mm diám con escultura evidente en el área marginal.

Distribución y ecología. *Amaranthus blitum* subsp. *emarginatus* se distribuye en regiones tropicales y templadas de ambos hemisferios, estando naturalizada en Europa (Carretero, 1990). Prefiere suelos húmedos, arenosos y fértiles (*Pedersen 10849*, LP; *Pedersen 1097*, CTES, LP). En el hemisferio sur florece entre los meses de octubre y mayo.

Discusión. Moquin (1849) describe *Euxolus viridis* var. *polygonoides* sobre la base de dos ejemplares: *Zollinger 1646* y *Salzmann 463*. Luego, Uline y Bray (1894b) transfieren *E. viridis* var. *polygonoides* al género *Amaranthus* y lo elevan a la categoría de especie con el nombre de *A. emarginatus*, debido a la existencia de *A. polygonoides* publicado por Linneo en 1759. Uline y Bray (1894b: 319) adjudicaron la publicación de *A. emarginatus* a Salzmann por Moquin como “*A. emarginatus* Salzm. ex Moq. l. c. 274”. El nombre *A. emarginatus* Salzm. fue citado por Moquin (1849: 274) como un sinónimo de *E. viridis* var. *polygonoides*, basado en el ejemplar *Salzmann 463* (que lleva el nombre “*Amaranthus emarginatus*” proba-

blemente escrito por el propio Salzmänn), por lo tanto la mención debió otorgarse a Salzmänn solamente.

Carretero (1985) realiza una nueva combinación elevando la variedad a la categoría de subespecie: *Amaranthus blitum* subsp. *polygonoides*. Sin embargo, este nombre constituye un homónimo posterior de *A. blitum* var. *polygonoides* Moq. (1849: 263) según lo establecido en el Art. 53.4 (McNeill et al., 2012), taxón este último que corresponde a *A. graecizans* subsp. *thellungianus* (Nevsky) Gusev. Finalmente, Carretero et al. (1987) basándose en la publicación de Uline y Bray (1894b), consideran que *A. emarginatus* Salzm. ex Uline & W. L. Bray es una subespecie de *A. blitum* y realizan una nueva combinación: *A. blitum* subsp. *emarginatus* (Uline & W. L. Bray) Carretero, Muñoz Garmendia & Pedrol.

Con respecto a la lectotipificación, Hüguin (1987) designa como lectotipo a un ejemplar de *Zollinger* depositado en P, sin brindar más detalles. No obstante, en el herbario P existen dos cartulinas que tienen como colector a Zollinger y que llevan el número 1646, lo que determina que deba realizarse una lectotipificación en segunda instancia. El ejemplar P [código de barras] P00572006 cuenta con la fecha en la etiqueta, pero la planta se encuentra desprovista de hojas e inflorescencias. En cambio en la etiqueta del ejemplar P [código de barras] P00572007, si bien figura el nombre y el número de colector, no figura la fecha; sin embargo, la planta está completa con numerosas hojas e inflorescencias por lo que aquí se la designa como lectotipo de *Amaranthus blitum* subsp. *emarginatus* en segunda instancia.

Ejemplares examinados. ARGENTINA. **Buenos Aires:** Pdo. Chacabuco, 1922, *C. L. Spegazzini* s.n. (LP); Pdo. Ensenada, Río Santiago, *A. L. Cabrera* 7940, 10214 (ambos en LP); Pdo. Las Flores, El Trigo, *A. L. Cabrera* 14724 (LP); Pdo. Tigre, *Lanfranchi* 522 (LP). **Córdoba:** Dep. Punilla, Sa. Chica, ca. Lago San Roque, *A. T. Hunziker* 6159, 6370 (ambos en CORD). **Corrientes:** Dep. Concepción, Carambola, *T. M. Pedersen* 10849 (CTES, LP); Dep. Esquina: Río Corrientes, *A. P. Rodrigo* 975 (LP); Dep. Goya, Isla del Diablo, *O. Boelcke* 1472 (CTES, SI); Dep. Grl. Paz, Grl. Paz, *T. Ibarrola* 9519 (CTES); Dep. Mburucuyá, Ea. Santa Teresa, *T. M. Pedersen* 1097 (CTES, LP); Dep. Mercedes, Mercedes, *A. Burkart* 29860 (CTES); Dep. San Cosme, Ingenio Primer Correntino, *B. Benítez et al.* 132 (CTES). **Formosa:** Dep. Pilcomayo, Ruta 86, Km. 35, *I. Morel* 5896 (LIL). **Salta:** Dep. Rosario de Lerma, El Manzano, *S. Zabala* 22 (LIL). **Tucumán:** Dep. Capital, San M. del Tucumán, *M. Lillo* 3814 (LIL). BRASIL. **Bahia:** In ruderatis, caulis adscendens, 1830, *Salzmänn* 463 (sintipo, *Euxolus viridis* var. *polygonoides*, G-DC no visto, imagen!). **Mato Grosso do Sul:** Corumbá, *A. Pott et al.* 2275 (CTES). PARAGUAY. **La Cordillera:** Barrerito ca. de Caacupú, *A. Burkart* 18232 (SI). **Misiones:** Santiago, Ea. La Soledad, *T. M. Pedersen* 8666 (CTES).

SUDÁFRICA. **North Cape:** Khamiesberg-Pauschoek-Slootjiesdam, *P. Carrick* 9 (NBG).

II. 5c. *Amaranthus blitum* L. subsp. *oleraceus* (L.)
Costea, *Sida* 19(4): 984. 2001. Basónimo: *Amaranthus oleraceus* L., *Sp. Pl.* ed. 2: 1403. 1763. *Albersia oleracea* (L.) Kunth, *Fl. Berol.* 2(2): 144. 1823. *Euxolus oleraceus* (L.) Moq. in de Candolle, *Prodr.* 13(2): 273. 1849. *Albersia blitum* var. *oleraceus* (L.) Hook. f., *Fl. Brit. Ind.* 4: 721. 1885. *Amaranthus lividus* L. var. *oleraceus* (L.) Thell., *Syn. Mitteleur. Fl.* 5 (Abth. 1): 321. 1919. *Amaranthus ascendens* Loisel. var. *oleraceus* (L.) Thell. ex Priszter, *Agrártud. Egyet. Kert-Szölőgazdaságtud. Karának Évk.* 2: 221. 1953. *Amaranthus lividus* L. subsp. *oleraceus* (L.) Soó, *Acta Bot. Acad. Sci. Hung.* 10: 376. 1964. TIPO: [India]. “Habitat in India”, *Herb. Linnaeus 1117.13* (lectotipo, designado por Fillias et al. [1980: 150], LINN 1117.13 no visto, imagen!).

Amaranthus lividus L., *Sp. Pl.* 990. 1753. *Euxolus lividus* (L.) Moq. in de Candolle, *Prodr.* 13(2): 273. 1849. TIPO: Estados Unidos de América. “Habitat in Virginia”, 1651, tab. s.n. de *Bahuin & Cherler* (lectotipo, designado por Reveal & Jarvis [2009: 978], lamina “*Blitum pulchrum rectum magnum rubrum*”, tab. s.n. en *Bahuin & Cherler*, 1651: 966).

Los tallos de *Amaranthus blitum* subsp. *oleraceus* son erectos y a menudo presentan tonalidades rojizas; sus frutos son mayores de 2 mm, rugosos, mientras que las semillas miden 1.2–1.6 mm diám y tienen escultura poco evidente en el área marginal.

Usos. Cultivada como hortaliza.

Distribución y ecología. De acuerdo con Costea et al. (2001c) *Amaranthus blitum* subsp. *oleraceus* se trata de un cultígeno, producto de la selección hecha sobre *A. blitum* subsp. *blitum*, existiendo solamente como hortaliza cultivada.

Discusión. Para el nombre *Amaranthus lividus* Aellen (1972) designó como material tipo al ejemplar *Herb. Linnaeus 1117.14* (LINN). Pero este ejemplar presenta una inscripción sobre su cartulina que dice *A. blitum* por lo que ha sido considerado como tipo de ese nombre de la especie. Con posterioridad, Townsend (1974b) designa un neotipo, lo cual en opinión de Jarvis et al. (2007) no correspondería ante la existencia de la lámina de Bauhin y Cherler. Finalmente, esta posición es reafirmada por Reveal y Jarvis (2009: 978) quienes designan como lectotipo a la lámina de Bauhin & Cherler que lleva la inscripción “*Blitum pulchrum rectum magnum rubrum*”.

II. 5d. *Amaranthus blitum* L. subsp. *pseudogracilis* (Thell.) N. Bayón, stat. nov. Basónimo: *Amaranthus lividus* L. f. *pseudogracilis* Thell., Syn. Mitteleur. Fl. 5 (Abth. 1): 321. 1919. *Amaranthus emarginatus* Uline & W. L. Bray subsp. *pseudogracilis* (Thell.) Hügin, Willdenowia 16: 463. 1987. *Amaranthus blitum* L. var. *pseudogracilis* (Thell.) Costea, Sida 19(4): 981. 2001. TIPO: Germany. Mecklenburg-Vorpommern: im Botanischen Garten Strasburg, 8 ago. 1904, A. Ludwig 12130 (lectotipo, designado por Iamónico [2014b: 5], B [código de barras] B100261513!; isoelectotipo, B [cb] B100261512!).

Los tallos de *Amaranthus blitum* subsp. *pseudogracilis* son ascendentes, vigorosos, con hojas de 2–4(–6) cm e inflorescencia larga, delgada y flexuosa de disposición terminal.

Distribución y ecología. *Amaranthus blitum* subsp. *pseudogracilis* es nativa de los trópicos e introducida en regiones templado cálidas de América del Norte y Europa. A veces crece como maleza de cultivos (Schulz 3296, 14712, CTES), prefiriendo suelos fértiles (Venturi 1957, LP, SI). En Argentina y Uruguay florece entre los meses de noviembre y marzo.

Ejemplares examinados. ARGENTINA. **Buenos Aires:** La Plata, N. D. Bayón 626 (LPAG); Los Hornos, N. D. Bayón 1332 (LPAG); C. L. Spegazzini s.n. (LP). **Chaco:** Colonia Benítez, A. G. Schulz 3296, 14712 (ambos en CTES); T. Meyer 4750 (LIL). **Córdoba:** Dep. Capital, Córdoba, en la Carolina, a orillas del Río Primero, A. T. Hunziker 19362, 24939 (ambos en CORD); Dep. Capilla del Monte, Los Cocos, Schiffmacher 629 (LP). **La Rioja:** Dep. Capital, A. T. Hunziker 4772 (CORD). **Santa Fe:** Dep. Capital, La Guardia, A. M. R. Huidobro 3085 (CTES, LIL). **Tucumán:** Dep. Capital, Río Salí, S. Venturi 1957 (LP, SI). URUGUAY. **Paysandú:** Río Uruguay, Isla Queguay, Rosen-gurt B-3805 (CTES).

II. 6. *Amaranthus brownii* Christoph. & Caum, Bernice P. Bishop Mus. Bull. 81: 25. 1931. TIPO: Estados Unidos de América. Islas Hawai: Nihoa Island, 17 abr. 1923, E. L. Caum 73 (holotipo, BISH-462208 no visto, imagen!; isotipos, NY [código de barras] NY00324464!, K [cb] K000190109 no visto, imagen!). Figura 23.

Hierba anual; tallos principales usualmente erectos, de 0.40–1 m, ramificados, sulcados, glabrescentes. Hojas con el pecíolo de 3–5 mm, glabras adaxialmente y glabras o glabrescentes abaxialmente, lámina linear a linear-lanceolada, no ondulada, 3–5.5(–6.5) × 0.2–0.3 cm, atenuada en la base, aguda en el ápice, con un mucrón de 0.3–0.4 mm.

Inflorescencias terminales y axilares, las primeras en espigas foliosas, a veces sin hojas en la porción distal y en glómérulos axilares; brácteas y bractéolas ovado-deltoides a oblongas, ± 1 mm, casi igualando a los sépalos, membranáceas, con la vena media marcada, mucrón 0.1–0.3 mm. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con 3 o 4 sépalos lanceolados, 1.3–1.4 × 0.4–0.8 mm, membranáceos con la vena media de color verde, 3 estambres. Flores pistiladas con 3 sépalos espatulados, 0.8–1 × 0.2–0.5 mm, membranáceos con la vena media conspicua, mucronados en el ápice; estigmas dos, 0.1 mm. Fruto indehiscente, rugoso; semillas de color castaño-negruzco, 1.3 × 1.5 mm, opacas.

Distribución y ecología. *Amaranthus brownii* es una especie endémica de las Islas Hawaii que crece entre los 100 m y 300 m. Prefiere lugares soleados, con suelos profundos y bien drenados. Florece entre abril y julio.

Discusión. Pese a que en la descripción original se menciona la posible semejanza de *Amaranthus brownii* con la especie australiana *A. interruptus* (bajo el nombre de *A. lineatus* R. Brown), se trata claramente de dos especies distintas. Las hojas lineares de *A. brownii* y las breves espigas terminales contrastan con las hojas ovadas, oblongas o rómbicas y las largas espigas terminales de *A. interruptus*. Además, *A. brownii* tiene tres sépalos en sus flores pistiladas mientras que la segunda cinco. Por otro lado, las dos especies con hojas lineares de las Islas Galápagos, esto es *A. sclerantoides* y *A. furcatus*, tienen su lámina dilatada en el ápice, carácter que no se observa en *A. brownii*.

Ejemplares examinados. ESTADOS UNIDOS DE AMÉRICA. **Islas Hawaianas:** Isla Nihoa, Miller Peak, near summit, D. Herz 1013 (BISH no visto, imagen!); Isla Nihoa, Middle Valley, D. Herbst & W. Takeuchi 6545 (BISH no visto, imagen!).

II. 7. *Amaranthus californicus* (Moq.) S. Watson, Bot. California [W. H. Brewer] 2: 42. 1880. Basónimo: *Mengea californica* Moq. in de Candolle, Prodr. 13(2): 270. 1849. TIPO: Estados Unidos de América. California: jul. 1846, K. T. Hartweg 1930 (holotipo, GDC [código de barras] G00201669 no visto, imagen!; isotipo, OXF no visto, imagen!). Figura 24.

Amaranthus carneus Greene, Pittonia 2: 105. 1890. TIPO: Estados Unidos de América. Idaho. Beaver Canyon, 1 ago. 1889, E. L. Greene s.n. (holotipo, NDG [código de barras] NDG15491 no visto, imagen!).

Amaranthus albomarginatus Uline & W. L. Bray, Bot. Gaz. 19: 318. 1894. TIPO: Estados Unidos de América. California: Monterey Co., Jolon, 1876, E. Palmer 456 (lectotipo, aquí designado, GH [dos plantas ubicadas

abajo a la izquierda de la cartulina] [código de barras] GH00036980!; isoelectotipo, US [cb] US00106227 no visto, imagen!).

Amaranthus microphyllus Shinnery, Sida 1: 248. 1964. TIPO: Estados Unidos de América. Texas: El Paso County, Hueco Mtns., 20 ago. 1946, U. T. Waterfall 6620 (holotipo, BRIT-23277 no visto, imagen!; isotipo, GH [código de barras] GH00037000!).

Hierbas anuales; tallos principales usualmente postrados, muy ramificados en la base, 10–50 cm, carnosos, blancuzcos, glabros. Hojas con pecíolo de hasta 9 mm, glabras, lámina linear, lanceolada, obovada o espatulada, ondulada, 2–15 × 1–8 mm, de color verde pálido, con la vena principal blancuzca en la cara abaxial, con una línea blancuzca en el margen, éste ondulado, cuneada en la base, obtusa o subaguda en el ápice, con un mucrón de 0.5–0.7 mm. Inflorescencias axilares, en glomérulos de 1–1.5 cm diám, esparcidos desde la base hasta el ápice de la planta; brácteas y bractéolas linear-lanceoladas, 0.5–1.4 mm, espinescentes. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con (2)3 sépalos lineares, o angostamente lanceolados u oblongos, (1)3 estambres. Flores pistiladas con 1–3 sépalos angostamente lanceolados, a menudo el más largo casi de la misma longitud que la bractéola, próximo a ella, 1–1.4 mm, con una arista corta o sin ella, agudos a acuminados, los otros sépalos reducidos, 0.4–1 mm, a veces incluso faltando; estigmas tres, 0.5–1 mm, curvos. Frutos dehiscentes, con el opérculo por lo general rugoso, urna lisa o rugosa, 1–1.3 mm; semillas de color castaño-rojizo, 0.9–1.2 mm diám, brillantes.

Distribución y ecología. *Amaranthus californicus* es conocida en América del Norte (Canadá y Estados Unidos de América). Prefiere planicies húmedas y alcalinas en la costa de lagos (*Belshaw* 2674, MO), aunque también banquinas de rutas, tierras cultivadas (*Moodie* 52, US) ambientes disturbados y zanjas de regadío (*Rust* 861, US). Esta especie crece entre el nivel del mar y los 2800 m (*Mosyakin & Robertson*, 2003). Florece entre los meses de julio y octubre.

Nombre vulgar. California amaranth (*Mosyakin & Robertson*, 2003).

Discusión. *Amaranthus californicus* se asemeja a *A. albus* por sus brácteas y bractéolas subuladas y espinescentes, más largas que los sépalos en las flores pistiladas (a veces en *A. californicus* un sépalo puede igualar a la bractéola) y por sus frutos dehiscentes. Sin embargo, *A. albus* presenta plantas erectas o ascendentes, con un número constante de tres sépalos en sus flores pistiladas los que son prácticamente iguales entre sí, mientras que en *A. californicus* los tallos son

postrados y los sépalos de las flores pistiladas desiguales en número de uno a tres.

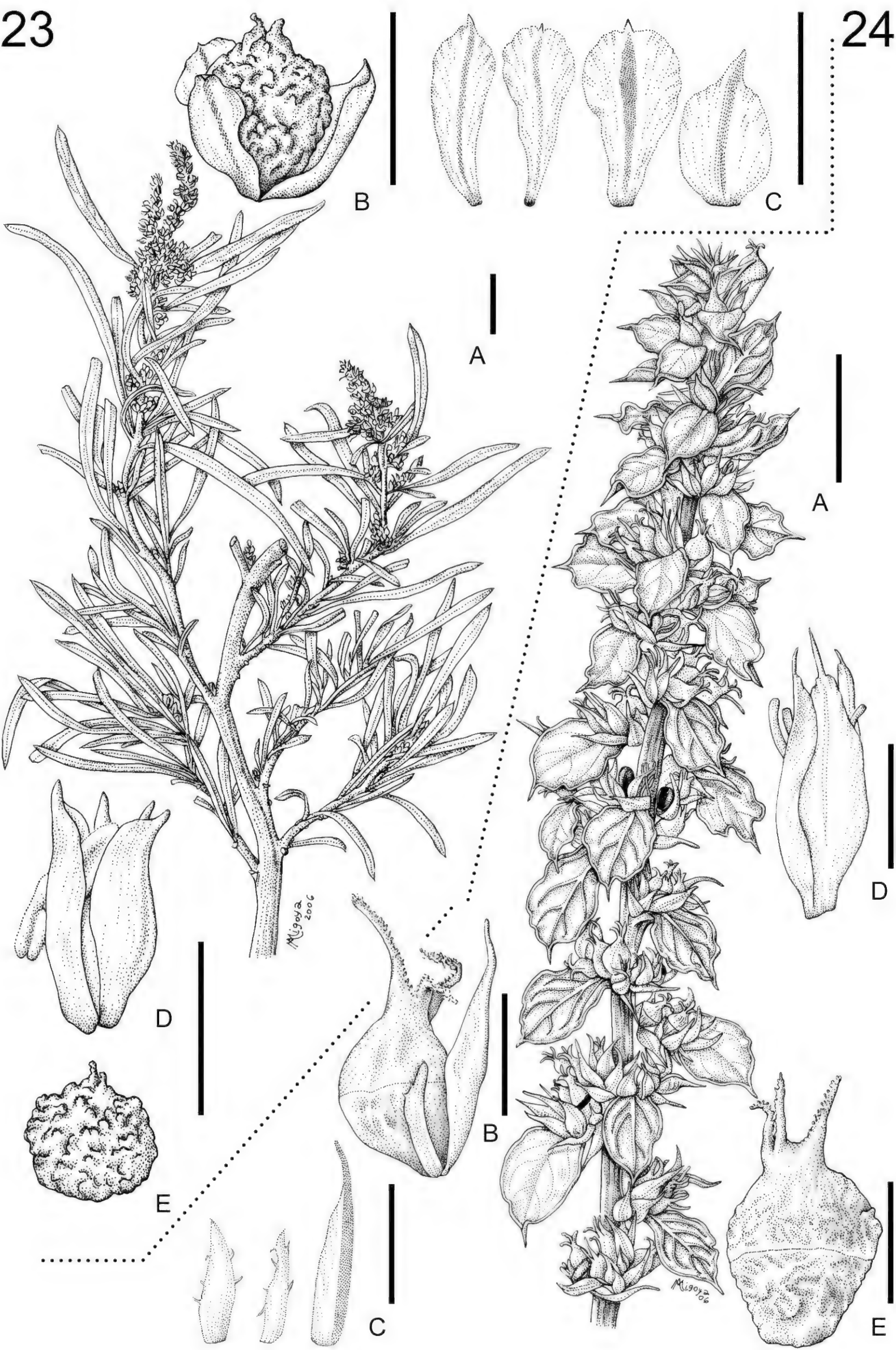
Greene (1890) describe *Amaranthus carneus* sobre la base de un ejemplar suyo, sin número, depositado en NDG, del que se ha estudiado la imagen. De acuerdo a los ejemplares examinados, los caracteres de *A. carneus* mencionados por Greene no permiten distinguir dicha especie de *A. californicus*, pues ambas especies poseen a menudo hojas obovadas, brácteas agudas y frutos lisos o apenas rugosos. Greene hace hincapié en las coloraciones rosadas y purpúreas de los tallos y envés foliar (de allí el nombre) que son muy comunes en *Amaranthus*, no resultando mayormente útiles al momento de diferenciar especies. Por lo antes expuesto, se decide seguir el criterio de Standley (1917) al considerar a *A. carneus* como un sinónimo de *A. californicus*.

Amaranthus albomarginatus fue descrito sobre la base del ejemplar *Palmer* 456, del que se han localizado dos duplicados, uno depositado en GH y el otro en US. Ambos cuentan con la información de colector y número, fecha y lugar de colección ajustándose a la descripción del protólogo. Sobre la cartulina del GH están montados tres ejemplares, uno de los cuales cuenta con dos plantas con abundantes estructuras vegetativas y reproductivas, que se corresponden con la colección de *Palmer* 456, el que aquí se designa como lectotipo de *A. albomarginatus*.

Ejemplares examinados. ESTADOS UNIDOS DE AMÉRICA. **California:** Merced Co., Tules N of Dos Palos, W. L. Jepson 13326 (CTES); Searsville, San Mateo Co., C. F. Baker 1855 (US); alkaline flats near Hanford, T. H. Kearney 81 (US); lower California, C. R. Orcutt 1015 (GH); S California, San Bernardino, S. B. & W. F. Parish 1143 (GH); lower SW-facing slope of Snow Mtn., 1 mi. NE of Potato Hill, C. M. Belshaw 2674 (MO); marshes of Sonoma Co., Laguna Santa Rosa, N Sebastopol, P. Rubtsoff 3864, 5240 (ambos en MO); Los Angeles Co., Puddingstone Reservoir near San Dimas, 20 oct. 1946, G. C. Fleischman s.n. (LIL). **Idaho:** Spencer, Burnside Ranch, H. J. Rust 861 (US). **Montana:** Bonner, Missoula Co., J. H. Handberg et al. 1044 (US). **Virginia:** Alberta, Cardston, M. E. Moodie 52 (US).

II. 8. *Amaranthus capensis* Thell., Syn. Mitteleur. Fl. 5 (Abth. 1): 293–294. 1919. TIPO: Alemania. Saxony-Anhalt, Rodleben, cerca de Rosslau, 1 ago. 1908, A. Zobel s.n. (lectotipo, designado por Bayón y Freire [2011: 174], Z [código de barras] Z-000000241!). Figura 25.

Hierba anual; tallos principales postrados, 5–25(–60) cm, más o menos ramificados, especialmente abajo, con pelos cortos y rectos o papiliformes cuando jóvenes. Hojas con pecíolo de 10–13 mm, glabras, lámina obovada, algo ondulada, 3–20 × 2–10 mm, atenuada en la base, obtusa en el ápice, redondeada o



apenas emarginada en el ápice, sin mucrón o con uno muy corto, con margen ondulado. Inflorescencias axilares, en glomérulos de 3–6 mm diám, agrupados hacia el ápice de los tallos, de color verdoso; brácteas y bractéolas lanceoladas a ovado-acuminadas, 1.2 mm, algo más cortas que los sépalos, membranáceas, pálidas, con el ápice reflejo. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con 3 sépalos ovado-elípticos, 2–2.25 mm, cortamente acuminados, 3 estambres. Flores pistiladas con 3 sépalos lanceolados a obovado-espátulados, 1.5–2.5(–5) mm, subiguales a marcadamente desiguales, estando 1 o 2 sépalos ensanchados en la mitad distal, con una zona de color verde, agudos a obtusos en el ápice, con un apículo de 0.1–0.25 mm, algunas veces conspicuamente reflejo; estigmas 3, rectos o algo reflejos, 0.5–1 mm. Frutos dehiscentes, lisos o con el opérculo rugoso, más cortos que los sépalos, adelgazados en un rostro apical; semillas de color negro y brillantes en el centro, de color castaño y semibrillantes en el área marginal, 0.9–1.3 mm diám, finamente reticuladas en el margen.

Discusión. *Amaranthus capensis* es a tal punto próxima a *A. dinteri*, que *A. capensis* subsp. *uncinatus* (Thell.) Brenan fue considerada como una variedad de esa especie hasta que Brenan (1981) la reubicó en su posición actual. *Amaranthus capensis* se diferencia de *A. dinteri* por tener los sépalos de las flores pistiladas lanceolados o espátulados, desde obtusos a acuminados, desiguales entre sí, uno o dos de ellos ensanchados distalmente. Contrariamente, *A. dinteri* tiene los sépalos de las flores pistiladas ovados u oblongos, acuminados, no ensanchados distalmente.

CLAVE PARA LA DIFERENCIACIÓN DE LAS SUBESPECIES DE
AMARANTHUS CAPENSIS

1. Sépalos de las flores pistiladas desiguales, de \pm 2–3.5 mm; 1 o 2 sépalos ensanchados y de color verde arriba, con apículo de 0.1–0.25 mm, a menudo curvo pero no subulado-uncinado; brácteas y bractéolas con el ápice agudo, breve y reflejo *A. capensis* Thell. subsp. *capensis*
- 1'. Sépalos de las flores pistiladas subiguales, (2.5–) 4–5.5 mm, gradualmente adelgazándose hacia el ápice en una punta alargada subulada de 1–2.5 mm, conspicuamente uncinada; brácteas y bractéolas subuladas
... *A. capensis* Thell. subsp. *uncinatus* (Thell.) Brenan

II. 8a. *Amaranthus capensis* Thell. subsp. *capensis*.

Los ejemplares de *Amaranthus capensis* subsp. *capensis* poseen las brácteas y bractéolas florales con el ápice agudo, breve y reflejo, siendo los sépalos de las flores pistiladas desiguales, 1 o 2 sépalos ensanchados y de color verde arriba, con apículo pero no subulados y uncinados.

Distribución y ecología. *Amaranthus capensis* subsp. *capensis* se distribuye en Sudáfrica y Lesotho, encontrándose al costado de las rutas y constituyéndose a veces en maleza (Brenan, 1981). Florece en enero.

Discusión. Brenan (1981: 474) menciona al ejemplar *Ecklon & Zeyher* 88 coleccionado en Sudáfrica como lectotipo de *Amaranthus capensis*, dejando explícito que él no vio el ejemplar. Se han consultado los herbarios NBG, S y STR donde se encuentran las colecciones de *Ecklon & Zeyher*, pero de acuerdo a sus curadores, en ninguno de ellos se halla depositado el ejemplar en cuestión. Por ese motivo, se designó como lectotipo al ejemplar *Zobel s.n.* (Z) el que forma parte del material citado por Thellung (1919a) en la descripción original y que corresponde con las características de la especie.

Ejemplares examinados. SUDÁFRICA. **Cape:** (Colesberg). A 14 km de Venterstad, en la ruta a Bethulie, *J. P. M. Brenan* 14089 (NBG); *K. L. P. Zeyher s.n.* (SAM-19198). **East Cape:** Aliwal North, Neuwe, Hantom, *Drège s.n.* (SAM 19199); Graaff Reinet, *Zeyher s.n.* (SAM 19198).

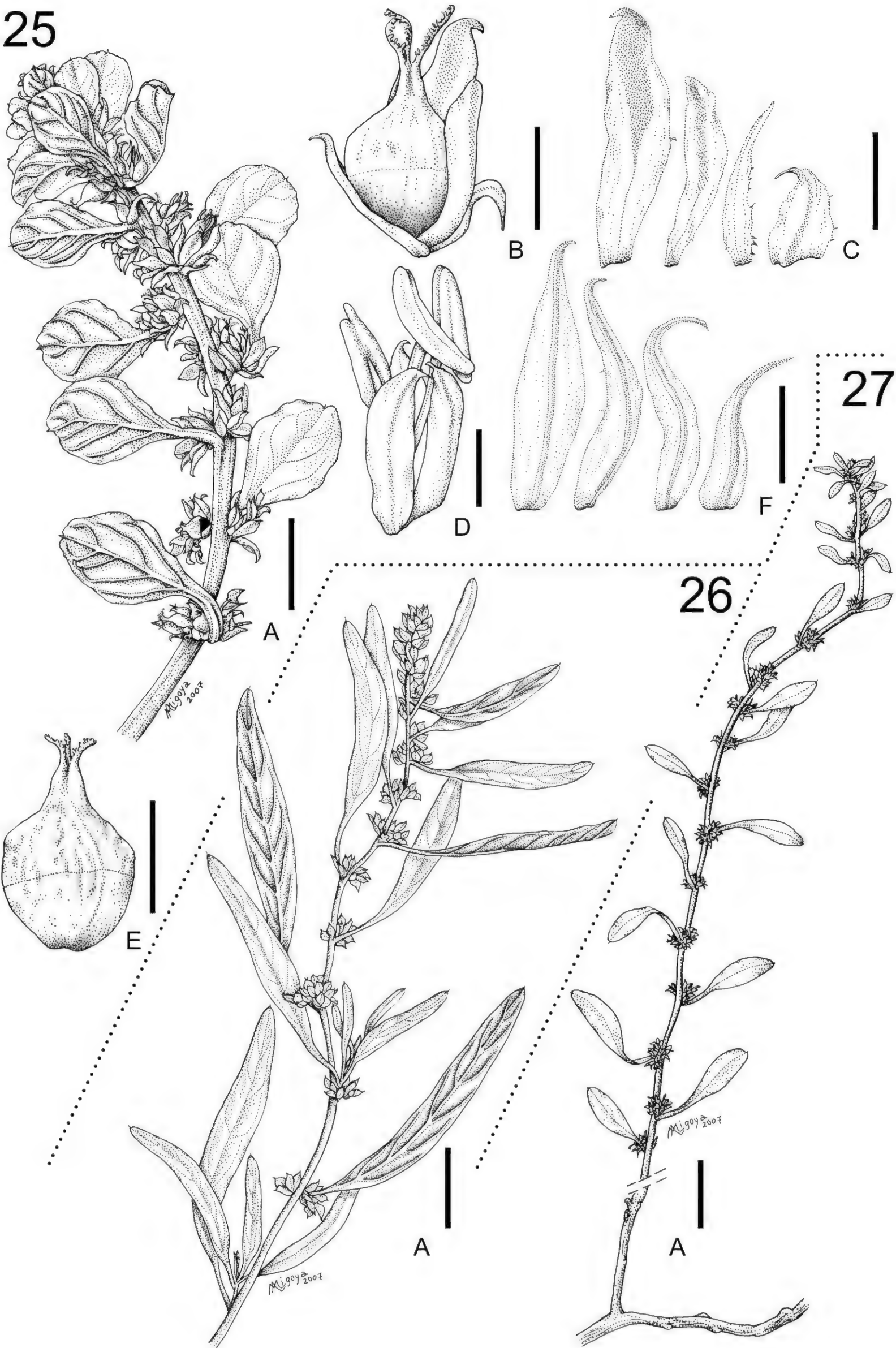
II. 8b. *Amaranthus capensis* Thell. subsp. *uncinatus* (Thell.) Brenan, J. S. African Bot. 47(3): 475. 1981. Basónimo: *Amaranthus dinteri* Schinz var. *uncinatus* Thell., Repert. Spec. Nov. Regni Veg. 13 (Abth. 5): 79. 1913. TIPO: Alemania. Lower Saxony, Döhren, ca. Hanover, jul. 1911, *J. Scheuermann s.n.* (lectotipo, designado por Bayón y Freire [2011: 174], Z [código de barras] Z000000245!).

Amaranthus capensis subsp. *uncinatus* se distingue por poseer brácteas y bractéolas florales subuladas, sépalos de las flores pistiladas subiguales, adelgazándose hacia el ápice en una punta alargada subulada, conspicuamente uncinada.

Distribución y ecología. Originaria de Sudáfrica, fue introducida en Europa como impureza en la lana ovina. Florece en julio.

←
Figura 23. *Amaranthus brownii* Christoph. & Caum. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. Ilustrado de *Christophersen & Caum* 73 (NY). La barra de escala para A = 1 cm; para B–E = 1 mm.

Figura 24. *Amaranthus californicus* (Moq.) S. Watson. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A–E, ilustrado de *Waterfall* 6620 (GH). La barra de escala para A = 5 mm; para B–E = 1 mm.



Nombre vulgar. Cape pigweed (Stace, 1991).

Ejemplares examinados. ALEMANIA. Schweiz, Desendiger, Kamgarn, *R. Probst* 2833 (SI).

II. 9. *Amaranthus centralis* J. Palmer & Mowatt, *Nuytsia* 19(1): 111. 2009. TIPO: Australia. Northern Territory: Todd River, ca. 9.6 km N Alice Springs, 10 nov. 1954, *G. Chippendale* 482 (holotipo, DNA no visto; isotipo, CANB no visto, imagen!).

Hierba anual; tallos principales erectos, de hasta 60 cm alt., angulosos, rojizos, con escasos pelos glandulares o glabros. Hojas con pecíolo de 2–20(–35) mm, lámina elíptica u ovada, más o menos ondulada, 6–35(–55) × 4–17(–25) mm, obtusa o emarginada en el ápice, mucronada, glabra o glabrescente. Inflorescencias axilares en glomérulos, algunas veces en espigas terminales erectas de hasta 6 cm; brácteas y bractéolas ovadas, 1.2–1.8 mm, más cortas que los sépalos, acuminadas, mucronadas. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con cáliz formado por 5 sépalos elípticos a angostamente obovados, 1.5–2 mm, obtusos a agudos, mucronados, con el margen membranáceo, blanquecinos, glabros, con el nervio medio delgado, de color verde, 3 estambres. Flores pistiladas con cáliz formado por 5 sépalos angostamente obovado-espátulados a espátulados, 2–4 mm, obtusos, mucronados, erectos o recurvos, de margen membranáceo, enteros, con la vena media ancha, 0.6–1 mm, de color verde; cuando en fruto los tépalos se endurecen en la zona inferior, siendo de color verde oscuro, castaño o pajizo, con los márgenes enteros, permaneciendo adheridos al fruto; estigmas 3, erectos o recurvos, 0.5 mm, algo inflados. Frutos indehiscentes, elipsoides, 1.5–3 mm, más cortos que los sépalos, algo rugosos, usualmente con costillas algo sobreelevadas, rectas, longitudinales, apenas tuberculadas; semillas de color castaño-rojizo a negro, lisas, brillantes.

Distribución y ecología. *Amaranthus centralis* es una especie originaria de Australia que crece en el sur del Northern Territory, y desde los montes Everard (cerca del Lago Eyre) hacia el sur hasta los montes Flinder en el norte de South Australia.

Asimismo, existen dos registros en el oeste de Queensland. Prefiere suelos de arenas rojas en cursos de agua estacionales, o suelos arenosarcillosos de la costa de ríos o cuerpos de agua permanentes. Florece y fructifica durante todo el año (distribución, hábitat y fenología tomados de Palmer, 2009).

Discusión. *Amaranthus centralis* es semejante a *A. induratus*, la que posee inflorescencias terminales densas o interrumpidas y glomérulos axilares (*A. centralis* posee espigas terminales sólo en forma ocasional), hojas lineares o angostamente oblongas u ovadas (*A. centralis* las tiene elípticas u ovadas) y los tépalos al momento de la fructificación presentan dientes en el margen (son enteros en *A. centralis*). Presenta ciertas semejanzas con *A. mitchellii* y *A. cuspidifolius*, aunque ambas poseen sépalos de las flores pistiladas espátulados a anchamente espátulados (siendo angostamente obovado-espátulados, obovado-espátulados a espátulados en *A. centralis*) y utrículos más pequeños carentes de costillas o si las tienen son muy prominentes y onduladas (pericarpio apenas rugoso, usualmente con costillas rectas poco marcadas en *A. centralis*).

II. 10. *Amaranthus clementii* Domin, *Biblioth. Bot.* 89: 76. 1921. TIPO: Australia. Western Australia. Entre los ríos Ashburton y De Grey, NW Australia [Western Australia], adquirido en ago. 1900, *E. Clement s.n.* [en herbario Domin 3793] (lectotipo, designado por Palmer [2009: 114], PR-526421 no visto, imagen!; isolectotipos, K [código de barras] K000357411 no visto, imagen!, K [cb] K000357412 no visto, imagen!). Figura 26.

Hierba anual; tallos principales erectos, usualmente ramificados, 20–40 cm, glabros, con hojas hasta el ápice. Hojas con pecíolo de 4–16 mm, glabras, lámina angostamente ovada, no ondulada, 2–5 × 0.3–1 cm, atenuada en la base y obtusa en el ápice, cara abaxial con las venas principales prominentes y blancuzcas. Inflorescencias principalmente terminales, sin hojas, en espigas elongadas o panículas, erectas, y también en glomérulos axilares de 0.5–1 cm diám; brácteas y bractéolas angosta-

Figura 25. *Amaranthus capensis* Thell. subsp. *capensis*. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. *Amaranthus capensis* subsp. *uncinatus* (Thell.) Brenan. —F. Sépalos y bráctea de la flor pistilada. A–E, ilustrado de *Brenan* 14089 (NBG); F, de *Probst* 2833 (SI). La barra de escala para A = 5 mm; para B–F = 1 mm.

Figura 26. *Amaranthus clementii* Domin. —A. Hábito fértil. A, ilustrado de *Clement s.n.* (PR). La barra de escala para A = 1 cm.

Figura 27. *Amaranthus cochleitepalus* Domin. —A. Hábito fértil. A, ilustrado de *Domin s.n.* (PR). La barra de escala para A = 1 cm.

mente ovado-lanceoladas, ± 2 mm, más cortas o a lo sumo iguales a los sépalos, membranáceas, ápice acuminado. Flores de ambos sexos en una misma inflorescencia. Flores estaminadas con 4 o 5 sépalos. Flores pistiladas con 4 o 5 sépalos obovados a obovado-espatulados, ± 3 mm, membranáceo-escaresos, blancuzcos, con la vena media marcada al momento de la fructificación, 0.3–0.8 mm ancho, y sus ramificaciones marcadas y de color verde, obtusos o apenas emarginados, reflejos, con el limbo de 1.2 mm de ancho en la porción distal, mucrón 0.1–0.3 mm; estigmas 3. Frutos dehiscentes, con el opérculo ruguloso, más cortos que el cáliz; semillas brillantes, 1.25–1.5 mm.

Distribución. *Amaranthus clementii* es endémica de la región de Pilbara (Western Australia), encontrándose a lo largo de la costa y en algunas islas, y en el continente desde Port Hedland hasta el río Murchison. También está presente en el Parque Nacional Río Rudall (distribución tomada de Palmer, 2009). Encontrada una vez en Gran Bretaña (Brenan, 1961) cuyas semillas habrían sido transportadas entre lana ovina.

Discusión. Por sus flores pistiladas *Amaranthus clementii* se asemeja a *A. undulatus*, habiendo sido considerada como variedad de la misma (aunque bajo el nombre de *A. pallidiflorus*). No obstante, *A. clementii* tiene hojas más anchas (no linear-lanceoladas) e inflorescencias terminales no foliosas o sólo foliosas en la base. Por sus hojas delgadas se asemeja a la especie sudamericana *A. persimilis*, pero en ésta última el ápice de las hojas es agudo y no obtuso, mientras que tiene frutos indehiscentes. También presenta cierta semejanza con *A. praetermissus* (sur de África) y con *A. blitoides* (de América del Norte). Las tres se parecen por sus hojas delgadas, sus inflorescencias en glomérulos axilares y sus frutos dehiscentes. Sin embargo, *A. clementii* tiene los sépalos de las flores pistiladas obtusos a emarginados, mientras que las otras dos especies los tienen agudos.

II. 11. *Amaranthus cochleitepalus* Domin, Biblioth. Bot. 89: 80. 1921. TIPO: Australia. Queensland: Pentland, feb. 1910, *Domin s.n.* (holotipo, PR-526427 no visto, imagen!). Figura 27.

Hierba anual; tallos principales decumbentes a erectos, ramificados, débiles, 15–20 cm, glabros. Hojas con pecíolo de hasta 5 mm, glabras, lámina oblonga, algo ondulada, 5–15 \times 2–4 mm, cuneada en la base, obtusa o apenas emarginada en el ápice, con un corto mucrón, flexible. Inflorescencias en glomérulos axilares; brácteas y bractéolas 1–1.2 mm,

apenas más cortas que el cáliz, membranáceas. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con 5 sépalos espatulados, agudos a obtusos, mucronados, 3 estambres. Flores pistiladas con 5 sépalos anchamente espatulados, 1.2–1.6(–2.3) mm, erectos, subiguales, 0.5 mm de ancho arriba, adelgazados en la base, 0.2 mm de ancho, blanquecinos, obtusos, con un breve apículo; estigmas 3, raramente 2. Frutos indehiscentes, 1–2.5 mm, rugosos, castaños, iguales o más largos que el cáliz; semillas castaño oscuro, 0.75–0.8 mm diám, brillantes.

Distribución y ecología. *Amaranthus cochleitepalus* es una especie australiana que crece en Port Hedland en la región de Pilbara (existe también un registro de la región de Kimberley) de Western Australia, en la Meseta Barkly, hacia el Sur hacia Alice Springs en el Northern Territory, y en Camooweal, al Sur del Golfo de Carpentaria y cerca de Clermont en Queensland (distribución tomada de Palmer, 2009). Florece entre los meses de marzo y mayo.

Discusión. *Amaranthus cochleitepalus* está estrechamente relacionada con *A. cuspidifolius*, aunque el cáliz de esta última especie tiene sépalos mucho más amplios, de 2.5–3.7 \times 1.5–1.8 mm de ancho distalmente, mientras que en *A. cochleitepalus* los sépalos tienen 1.2–1.6 \times 0.5 mm de ancho distalmente.

Ejemplares examinados. AUSTRALIA. **Northern Territory:** Bottle Waterhole, Lander River, *P. K. Latz 16141* (MEL no visto, imagen!). **Queensland:** 3 mi. N of Buchanan Creek, *G. Chippendale 1881* (NSW no visto, imagen!).

II. 12. *Amaranthus crassipes* Schltdl., Linnaea 6: 757. 1831. *Euxolus crassipes* (Schltdl.) Hieron., Bol. Acad. Nac. Córdoba 4: 13. 1881. *Scleropus crassipes* (Schltdl.) Moq. in de Candolle, Prodr. 13(2): 271. 1849. TIPO: Estados Unidos de América. Islas Vírgenes: St. Thomas Island, 1826–1828, *C. Ehrenberg s.n.* (holotipo, HAL-076208 no visto, imagen!). Figura 28.

Hierba anual; tallos principales decumbentes, algunas veces inicialmente erectos, 0.1–0.4(–0.5) m, ramificados en la base, estramíneos, glabros. Hojas con pecíolo de 10–30 mm, glabras, lámina angostamente a ampliamente obovada, casi orbicular, ovada, elíptica, no ondulada, 1.5–3 \times 0.5–2 cm, cuneada o algunas veces atenuada en la base, obtusa, redondeada o emarginada en el ápice, con un mucrón de 0.2 mm. Inflorescencias axilares, en glomérulos

que arrancan desde la base y llegan hasta el ápice de los tallos, 4–9 mm diám, con los ejes engrosados y endurecidos, 0.9–1.2 mm diám; brácteas y bractéolas anchas y deltoides, aquilladas, 0.5–1.25 mm, más cortas que los sépalos, membranáceas, vena media gruesa. Flores de ambos sexos sobre una misma inflorescencia. Flores estaminadas con 5 sépalos lanceolados, 1–1.5 mm, membranáceos, con la vena media de color verde, 3 estambres. Flores pistiladas con 5 sépalos angostamente espatulados, 1.2–2 mm, adelgazándose en una uña en al menos la mitad inferior, engrosados y unidos en la base, agudos y algo reflejos apicalmente; estigmas dos(tres), 0.75 mm. Frutos indehiscentes, más cortos que los sépalos, usualmente lisos en la base y tuberculados arriba, con un par de estilos lirados (raro 3), dispuestos sobre un rostro; semillas de color negro en el centro, y castaño-rojizo en el margen, 0.9–1.3 mm diám, poco brillantes.

Discusión. *Amaranthus crassipes* es muy similar a *A. scleropoides* tanto en sus órganos vegetativos como reproductivos. Vegetativamente, *A. scleropoides* presenta plantas más erectas y más altas. Sus frutos son dehiscentes, de pericarpio tuberculado, o liso por arriba de la línea de dehiscencia y con dos o tres ramas estigmáticas. Por su lado, las plantas de *A. crassipes* son hierbas de hábito decumbente, sus frutos son indehiscentes, de pericarpio conspicuamente tuberculado en la mitad superior y con dos (raro tres) ramas estigmáticas.

CLAVE PARA LA DIFERENCIACIÓN DE LAS SUBESPECIES DE
AMARANTHUS CRASSIPES

- 1. Lámina foliar ovada a anchamente ovada, algunas veces casi orbicular u obovada, 10–15 mm de ancho; cara abaxial de color verde o verde-amarillento *A. crassipes* Schltdl. subsp. *crassipes*
- 1'. Lámina foliar angostamente elíptica o angostamente obovada, 6–10 mm de ancho; cara abaxial de color verde glauco *A. crassipes* Schltdl. subsp. *warnockii* (I. M. Johnst.) N. Bayón

II. 12a. *Amaranthus crassipes* Schltdl. subsp. *crassipes*.

Amaranthus crassipes subsp. *crassipes* posee lámina foliar ovada o anchamente ovada, casi orbicular, u obovada, con la cara abaxial de color verde o verde-amarillento.

Distribución y ecología. *Amaranthus crassipes* subsp. *crassipes* se distribuye por el Mar Caribe, sur de Estados Unidos de América (desde Florida a Texas), México, Indias Occidentales y el norte de

Sudamérica (Colombia, Perú y Venezuela) (Henrickson, 1999). Constituye una maleza de caminos y lugares donde se acumulan desperdicios, en campos de pastoreo, en planicies arcillosas, limosas y a veces arenosas, en playas, y en laderas rocosas. Crece entre el nivel del mar y los 1300 m (Mosyakin & Robertson, 2003). Florece entre los meses de julio y diciembre.

Nombres vulgares. Clubfoot amaranth, spreading amaranth, tropical spreading amaranth (Mosyakin & Robertson, 2003).

Ejemplares examinados. VENEZUELA. **Nueva Esparta:** Isla de Margarita, El Valle, O. O. Miller & J. R. Johnston 29 (MO). **Vargas:** Parroquia Catia la Mar, N. Ramírez 2574 (CTES).

CUBA. Ca. La Habana, Curtiss 559 (SI).

ESTADOS UNIDOS DE AMÉRICA. **Islas Vírgenes:** Saint Thomas, B. Eggers 96 (CORD). **Texas:** Almite Canyon Co., R. Runyon 2345 (LP).

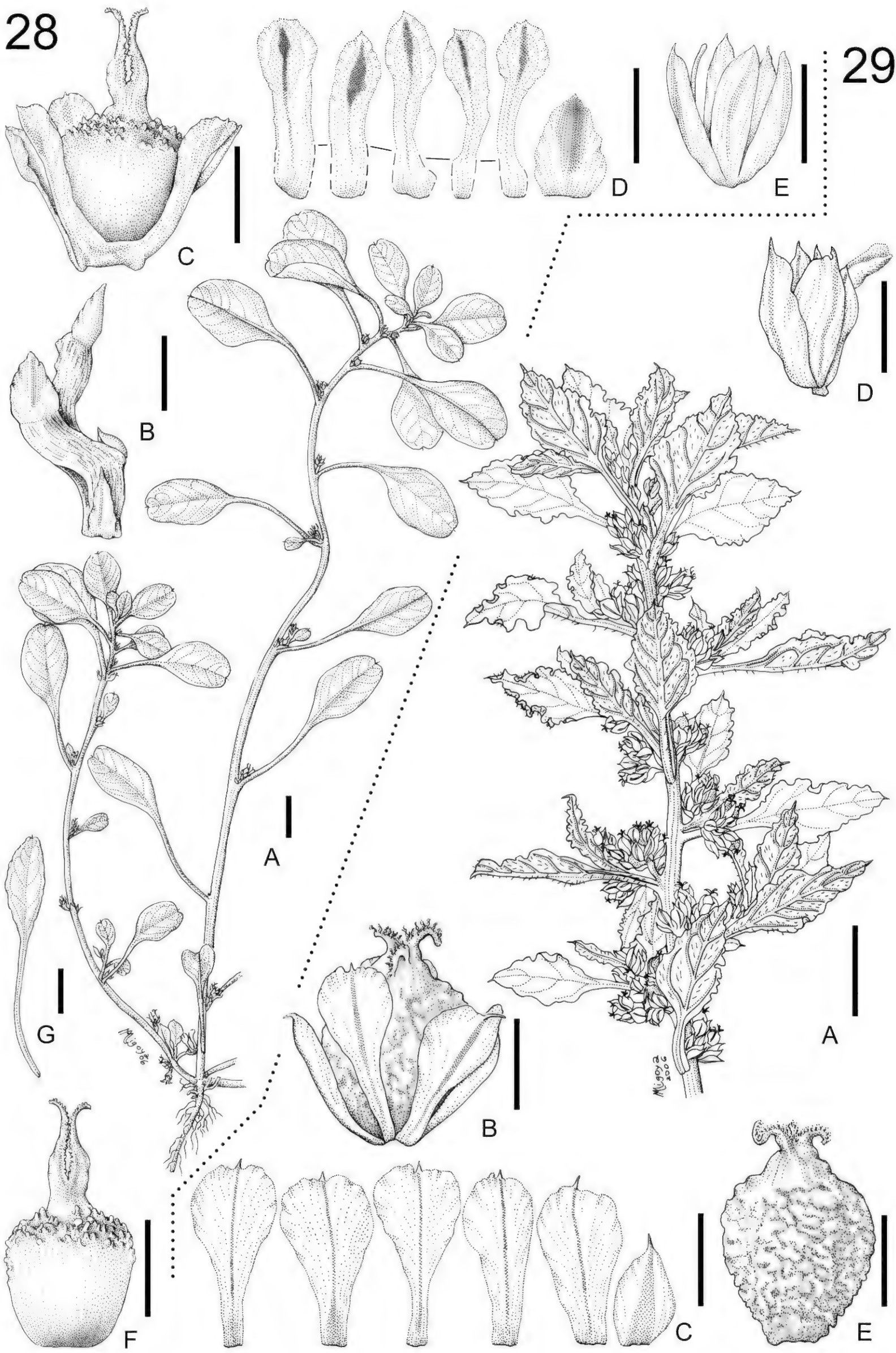
II. 12b. *Amaranthus crassipes* Schltdl. subsp. *warnockii* (I. M. Johnst.) N. Bayón, stat. nov. Basónimo: *Amaranthus warnockii* I. M. Johnston, J. Arnold Arbor. 25: 153. 1944. *Amaranthus crassipes* Schltdl. var. *warnockii* (I. M. Johnst.) J. Henrickson, Sida 18(3): 788. 1999. TIPO: México. Coahuila: W Coahuila, 1 mi. SE of Ocampo, silty plain near mogote, 8 sep. 1941, I. M. Johnston 8886 (holotipo, GH [código de barras] GH00037034!).

Amaranthus crassipes subsp. *warnockii* se caracteriza por tener hojas largamente pecioladas, con la lámina angostamente obovada de color verde glauco.

Distribución y ecología. *Amaranthus crassipes* subsp. *warnockii* se distribuye por el sudoeste de Texas (Estados Unidos de América) y en el desierto de Chihuahua (Henrickson, 1999: 788), al este del estado de Chihuahua y en el de Coahuila (México). Esta subespecie prefiere planicies abiertas, matorrales de *Prosopis* L. (Fabaceae) y áreas anegadas, y se encuentra hasta los 1300 m (Henrickson, 1999). Florece en agosto.

Ejemplar examinado. MÉXICO. **Coahuila:** rd. from Piedras Negras S to Monclova, I. M. Johnston 7076 (SI).

II. 13. *Amaranthus crispus* (Lesp. & Thévenau) A. Braun ex J. M. Coult. & S. Watson, Manual (Gray), ed. 6: 428. 1890 [feb.]. Basónimo: *Euxolus crispus* Lesp. & Thévenau, Bull. Soc. Bot. France 6: 656. 1859. TIPO: Francia. Languedoc-Roussillon: “lavoir à laine de Bessan”, 12 oct. 1858, A. V. Thévenau s.n. (lectotipo, designado por Iamónico [2014: 9], P [ejemplar de la izquierda] [código de barras]



P00572004 no visto, imagen!; isoelectotipos, BAA [cb] BAA00004361 no visto, imagen!, GH [cb] GH00037036 no visto, imagen!, P [cb] P00572005 no visto, imagen!). Figura 29.

Amaranthus crispus N. Terracc., Atti Accad. Sc. Napoli Ser. 2, 4: 188. 1890 [jul.], nom. illeg. TIPO: Italia. Lazio: Frosinone, “ad vias in submontosis Campaniae fontanaliri”, sep. 1821, *N. Terracciano s.n.* (lectotipo, designado por Iamónico [2014b: 3], FI, imagen!).

Hierba anual; tallos principales decumbentes o ascendentes, 10–40 cm, ramificados desde la base, pubescentes. Hojas con pecíolo de 2–10 mm, pubescentes en la cara abaxial, lámina ovada, romboide o lanceolada, ondulada, 4–13 × 2–10 mm, cuneada en la base, aguda u obtusa en el ápice, mucronada. Inflorescencias axilares, en glomérulos, algunas veces en una corta pseudoespiga foliosa; brácteas y bractéolas oblongas u ovadas, 0.8–1.4 mm, más cortas que los sépalos, membranáceas, ápice mucronado. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con 5 sépalos obovado-oblongos, 1.3–1.8 mm, obtusos, 1-nervados, mucronados, 5 estambres. Flores pistiladas con 5 sépalos espatulados u obovados, 1.3–2 mm, 1-nervados, obtusos a emarginados en el ápice, no reflejos, mucronados; estigmas tres, 0.3 mm. Frutos indehiscentes, poco más largos que los sépalos, enteramente rugosos; semillas de color castaño-rojizo, 0.9–1.1 × 0.7 mm, brillantes, lisas en el centro y con el margen punteado.

Distribución y ecología. *Amaranthus crispus* es nativa de Sudamérica, principalmente de Argentina, y Uruguay. Naturalizada en Europa (Pedersen, 1994). Se encuentra a menudo sobre suelos arenosos y pedregosos, en cultivos y rastros de cultivos (*Williamson 1115*, BAB; *Gutiérrez 137*, CTES). Crece entre el nivel del mar y los 1800 m (*García 156*, LP). En Argentina y Uruguay florece entre los meses de noviembre y marzo (mayo), mientras que en Europa lo hace entre los meses de junio y agosto.

Nombre vulgar. Crisp-leaved amaranth (Mossyakin & Robertson, 2003).

Discusión. *Amaranthus crispus* se asemeja a *A. standleyanus*, aunque esta última se caracteriza por presentar la lámina foliar algo crespa y con pecíolo

mayor a 1.8 cm, con los sépalos reflejos (alejándose del fruto a la madurez). *Amaranthus crispus* por el contrario tiene láminas foliares crespo-onduladas, pecíolos menores de 10 mm y sépalos aplicados al fruto cuando maduro.

Tanto Terracciano como Coulter y Watson trasladaron esta especie al género *Amaranthus* en el año 1890. Coulter y Watson lo hicieron en el mes de febrero y Terracciano en el mes de junio, por lo que los primeros autores tienen prioridad.

Ejemplares examinados. ARGENTINA. **Buenos Aires:** Pdo. Balcarce, *R. Martínez Crovetto 1488* (BAB); Pdo. Capitán Sarmiento, *E. D. Gautier s.n.* (BAB 62229); Pdo. Chascomús (LP); Pdo. B. Juárez, Sa. de la Tinta, Co. El Sombrerito, *D. Abbiatti 4447* (LP); Pdo. Grl. Pinto, 10 ene. 1898, *C. Hicken s.n.* (SI); Pdo. Grl. Pueyrredón, Mar del Plata, *A. Gallardo 160* (BAB); Pdo. La Plata, La Plata, entre Villa Elisa y Punta Lara, *A. L. Cabrera 7570* (LP); Pdo. Lobería, Lobería, feb. 1918, *A. Scala s.n.* (LP); Pdo. Monte Hermoso, Monte Hermoso, 1916, *E. Carotte s.n.* (LP); Pdo. Patagones, Carmen de Patagones, feb. 1898, *C. L. Spegazzini s.n.* (LP); Pdo. Tornquist, Sa. de la Ventana, nov. 1895, *C. L. Spegazzini s.n.* (LP); Sa. de la Ventana, 9 feb. 1901, *Hicken s.n.* (SI); Sin Pdo., entre Bahía Blanca y Río Colorado, ene. 1898, *C. L. Spegazzini s.n.* (LP). **Catamarca:** Dep. Andalgalá, Andalgalá, *Jørgensen 1689* (SI); Dep. Ancasti, Sa. de Ancasti, Dique de Ipizca, *A. T. Hunziker & A. E. Cocucci 15736* (CORD). **Chubut:** Dep. Viedma, Puerto Madryn, *J. Daciuk 726* (LP). **Córdoba:** Dep. Capital, Argüello, *J. Gutiérrez 137* (CTES); Dep. Cruz del Eje, entre los Ríos Guasta y Chaves, *A. T. Hunziker 8821* (CORD); Dep. Minas, Cordón Occidental, La Bismutina, *A. Castellanos 47715* (BA); Dep. Pocho, Ea. Orco-Suni, al pie del Co. Yerba Buena, *A. T. Hunziker 9846* (CORD); Dep. Punilla, falda E de la Sa. Chica, NO del Lago San Roque, *A. T. Hunziker 6364* (CORD); ca. del Río San Roque, al O de Villa Carlos Paz, *A. T. Hunziker 12285* (CORD); Dep. Río Primero, Ea. San Teodoro, *A. T. Hunziker 11924* (CORD). **La Pampa:** Dep. Caleu-Caleu, *N. H. Bartlett 19933* (SI); Dep. Chical C6, 20 km al S del Co. Centinela, *T. M. Pedersen 13326* (CTES); Dep. Lihuel Calel, ladera S-SO de las sierras, 29 ago. 1975, *H. E. Erb s.n.* (CTES); Dep. Loventué, Loventué, *Fortuna 119* (BA); Dep. Mara C6, Grl. Pico, *J. Williamson 1115* (BAB); Dep. Toay, Anquilobo, *C. B. Villamil & M. G. Cazzaniga 3852* (CTES); Dep. Utracán, Grl. Acha, *de la Rúa 1909* (SI). **La Rioja:** Dep. Gdor. Gordillo, Chamical, Ruta Nac. 79, entre el empalme con Ruta Nac. 38 y Salina La Antigua, *F. Biurrun & E. Pagliari 2211* (CORD). **Mendoza:** Dep. Alvear, La Escondida, *F. A. Roig 8884* (CTES); Dep. Las Heras, Uspallata, *E. M. García 156* (CTES); Dep. Luján, Luján de Cuyo, 5 dic. 1902, *L. Garola s.n.* (BAB); Dep. San Carlos, San Carlos, sobre Ruta 40, *F. A. Roig 5179* (CTES); Dep. San Martín, San Martín, 17 feb. 1901, *C. L. Spegazzini s.n.* (BAB). **Río Negro:** Dep. Conesa, Boca de la Travesía, Ruta 303, 16 dic. 1982, *S. Crespo & P. Calieres s.n.* (BAB); Dep. Valcheta, Sa. Pailemán,

Figura 28. *Amaranthus crassipes* Schldtl. subsp. *crassipes*. —A. Hábito fértil. —B. Eje de la inflorescencia. —C. Flor pistilada. —D. Sépalos y bráctea de la flor pistilada. —E. Flor estaminada. —F. Fruto. *Amaranthus crassipes* subsp. *warnockii* (I. M. Johnst.) N. Bayón. —G. Hoja. A–F, ilustrado de *Curtiss 559* (SI); G, de *Johnston 7076* (SI). Las barras de escala para A, G = 1 cm; para B–F = 1 mm.

Figura 29. *Amaranthus crispus* (Lesp. & Thénau) J. M. Coult. & S. Watson. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A, ilustrado de *Cabrera 7570* (LP); B, C, E, de *Daciuk 726* (LP); D, de *Bartlett 19933* (SI). La barra de escala para A = 5 mm; para B–E = 1 mm.

B. Piccinini & A. Leguizamón 2064 (BAB, CTES). **San Luis:** Dep. Ayacucho, Santa Rosa, *J. R. Báez 101* (SI); Dep. General Pedernera, Villa Mercedes, *G. Covas 1049* (LP); Villa Mercedes, *A. Burkart 10878* (CTES); Nueva Escocia, *A. Burkart 10849* (CTES); Dep. La Capital, Chischaca, 13 dic. 1925, *A. Castellanos s.n.* (BA-25/2807). **URUGUAY. Montevideo:** Montevideo, feb. 1876, *Gibert s.n.* (LP).

ESLOVAQUIA. Král'ovsky Chlmec, *Chrték 303* (BAB). **HUNGRÍA.** Cerca de Budapest, *A. Degen 138* (LIL); Syör, *S. Pólgar 2834* (SI).

II. 14. *Amaranthus cuspidifolius* Domin, Biblioth. Bot. 89: 78. 1921. TIPO: Australia. Western Australia: entre los ríos Ashburton y De Gray [O de Australia], ago. 1900, *E. Clement s.n.* (holotipo, PR-526426 no visto, imagen!). Figura 30.

Hierba anual; tallos principales erectos, decumbentes a ascendentes, 20–30(–50) cm, estriados, bastante ramosos, glabros. Hojas con pecíolo de 2–4(–8) mm, un tanto discoloras, algo glaucas y con las venas blanquecinas en el envés, glabras, lámina oblongo-elíptica, no ondulada, 5–18(–40) × 3–6(–12) mm, atenuada en la base, obtusa a emarginada en el ápice, mucrón 0.7 mm. Inflorescencias en glomérulos axilares, de 0.5 cm diám, a veces agrupándose en las porciones distales de los tallos, donde las hojas se tornan menores, originando pseudoespigas simples, densas; brácteas y bractéolas oblongo-lanceoladas a ovadas, 1–2 mm, más cortas que el cáliz, membranáceas, con la vena media de color verde, ápice acuminado. Flores de ambos sexos sobre la misma inflorescencia. Flores estaminadas con 5 sépalos oblongo-lanceolados, 2.2–2.5 mm, agudos, membranáceos con la vena media verdosa, mucrón 0.2–0.3 mm, 3 estambres. Flores pistiladas, con 5 sépalos anchamente espatulados, obovado-espatulados u orbicular-obtrulado-espatulados, 1.5–3 mm, limbo de 1.5–1.8 mm de ancho, adelgazados en la base, 0.2–0.3 mm de ancho, recurvos, con la vena media ramificada de color verde, obtusos a apenas emarginados, mucrón 0.2 mm; estigmas tres, 0.75 mm, engrosados en la base. Frutos indehiscentes, 1–2.5 mm (sin considerar los estilos), globosos u obovoides, rugosos, castaño-verdoso-oscuros; semillas de color negro en el área central, castaño oscuro en el área marginal, 1.25 mm diám, brillantes en el centro y opacas en el margen.

Distribución y ecología. *Amaranthus cuspidifolius* crece en la región de Pilbara (Western

Australia), en el Este en los desiertos de Sandy y Gibson y en las cadenas montañosas del Sur del Northern Territory, en el Norte de South Australia al Sur de Oodnadatta y los montes Flinders, en Nappa Merri en el Sudoeste de Queensland, y ca. de Broken Hill y Louth en el Oeste de New South Wales. Prefiere suelos rocosos o de arenas rojas (distribución y hábitat tomados de Palmer, 2009). Florece y fructifica en los meses de junio y julio.

Discusión. *Amaranthus cuspidifolius* es cercana a *A. mitchellii*, aunque sus hojas mucronadas y su pericarpio carente de costillas longitudinales permite una clara distinción.

Ejemplares examinados. **AUSTRALIA. New South Wales:** ca. Far Western Plains, Broken Hill, jun. 1919, *A. Morris s.n.* (NSW). **Northern Territory:** Mt. Olga (Kata Tjutal), *G. Chippendale 4668* (NSW). **South Australia:** 38 mi. SO de Ernabella, ca. Mt. Woodroffe, *F. J. Jurvey 11162* (NSW).

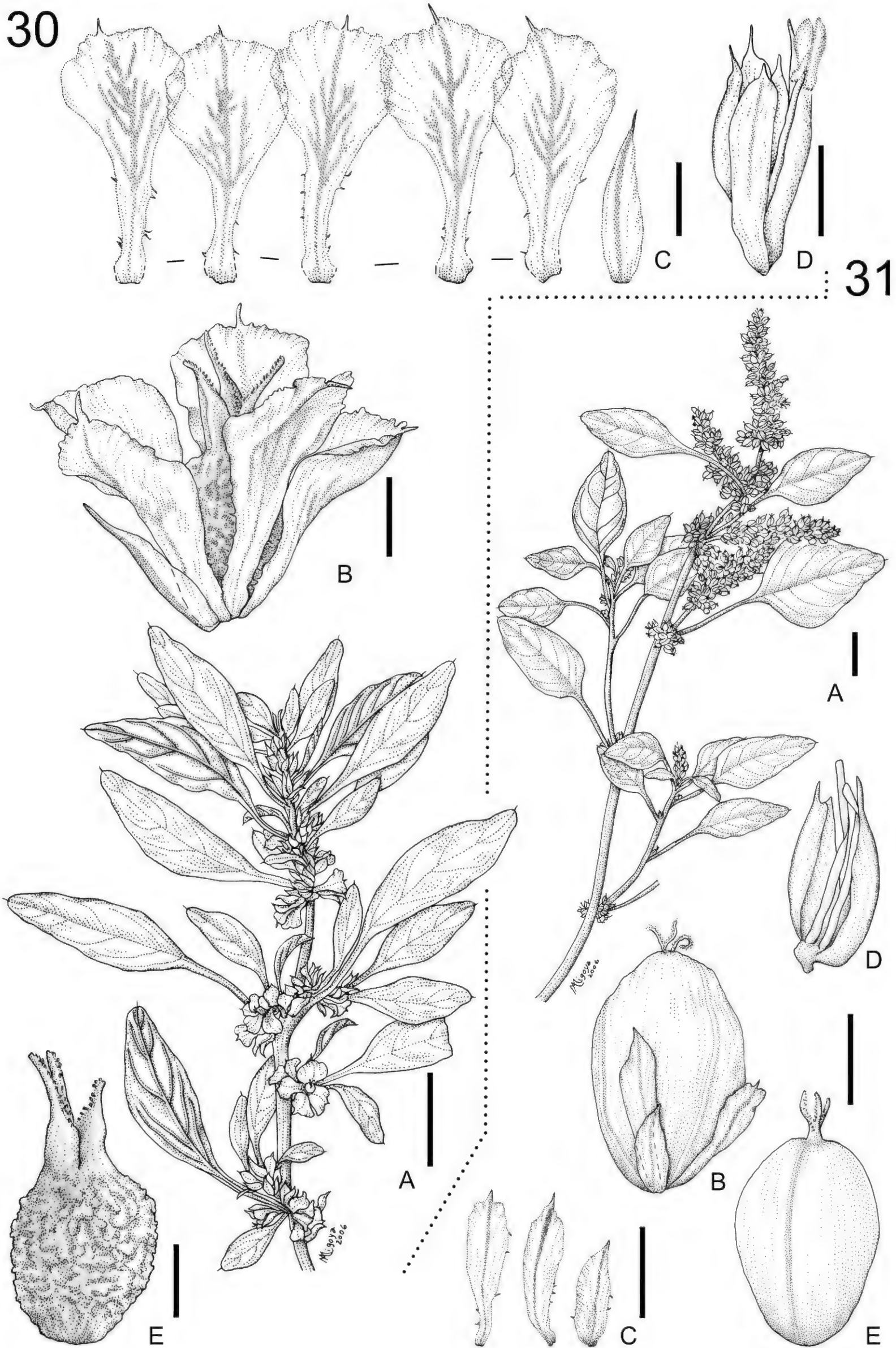
II. 15. *Amaranthus deflexus* L., Mant. Pl. Altera: 295. 1771. *Euxolus deflexus* (L.) Raf., Fl. Tellur. 3: 42. 1837. *Glomeraria deflexa* (L.) Cav., Descr. Pl. 319. 1802. *Albersia deflexa* (L.) Fourr., Ann. Soc. Linn. Lyon, sér. 2, 17: 142. 1869. TIPO: [País no conocido]. *Herb. Linnaeus 1117.18* (lectotipo, designado por Aellen [1972: 7], LINN 1117.18 no visto, imagen!). Figura 31.

Amarantellus argentinus Speg., Comun. Inst. Nac. Invest. Ci. Nat., Ser. Ci. Bot. 1: 344. 1901. TIPO: Argentina. Buenos Aires: Patagones, La Pantanosa, feb. 1898, *C. L. Spegazzini s.n.* (lectotipo, aquí designado, LPS-12072 en LP [código de barras] LP002713!).

Hierba anual o perenne de corta vida; tallos postrados o ascendentes, de hasta 60 cm, delicados a fuertes, ramificados desde la base, glabros o glabrescentes, hasta densamente pubescentes especialmente cuando jóvenes. Hojas con pecíolo de 5–20 mm, pubescentes a lo largo de la vena principal en la cara abaxial, lámina de forma variable: romboidal, ovoide, elíptica o lanceolada, no ondulada, 1–4.5 × 0.5–2.5 cm, cuneada a cuneado-subtruncada en la base, subaguda a obtusa y algunas veces apenas emarginada hacia el ápice, mucronulada. Inflorescencias terminales y axilares, las primeras en panojas piramidales compactas, 3–10 × 0.4–1.2 cm, sin hojas en la porción distal, y las segundas en glomérulos axilares; brácteas y bractéolas ovadas, 0.8–1.1 mm,

Figura 30. *Amaranthus cuspidifolius* Domin. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A–E, ilustrado de *Jurvey 11162* (NSW). La barra de escala para A = 1 cm; para B–E = 1 mm.

Figura 31. *Amaranthus deflexus* L. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A–E, ilustrado de *Fabris 6055* (LP). La barra de escala para A = 1 cm; para B–E = 1 mm.



aproximadamente la mitad de la longitud del cáliz, membranáceas, con la vena media verdosa, mucronuladas en el ápice. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas pocas, con 2(3) sépalos oblongo-lanceolados, acuminados, ca. 1 mm, estambres 2 o 3. Flores pistiladas con 2(3) sépalos lineares, linear-lanceolados, lanceolados u oblongo-lanceolados, 1.3–2 mm, agudos y acuminados a obtusos, con la vena media de color verde; estigmas 2 o 3, delgados, 0.25–0.4 mm. Fruto indehiscente, liso, elipsoide o piriforme, 1.7–3 mm, casi el doble de la longitud del cáliz, redondeado u obtuso en el ápice; semillas castaño-rojizas a negruzcas, $1-1.2 \times 0.7-0.8$ mm, brillantes en la zona central y reticuladas en la zona marginal.

Distribución y ecología. *Amaranthus deflexus* es nativa de América del Sur. Se encuentra ampliamente distribuida en regiones subtropicales y templadas de todo el mundo. Es una planta ruderal, que crece sobre lomadas de conchillas y banquinas de caminos (*Ringuelet* 325, LP), considerada a veces maleza invasora, común en suelos sueltos y modificados. Crece entre el nivel del mar y los 500 m (Pedersen, 1994; Mosyakin & Robertson, 2003). En Argentina florece entre los meses de noviembre y mayo.

Nombres vulgares. Bledo, tomatillo, yuyo rastro (Fabris, 1967); Argentina amaranth, deflexed amaranth, low amaranth, large-fruit amaranth (Mosyakin & Robertson, 2003).

Usos. Empleada en medicina popular como diurética, laxante y emoliente (Toursarkissian, 1980).

Discusión. *Amaranthus deflexus* es una especie característica por sus frutos lisos y mayores que los sépalos. El primer carácter lo comparte con *A. lombardoi*, mientras que el segundo lo hace con *A. macrocarpus*. De la primera especie se la puede distinguir claramente pues *A. deflexus* cuenta con dos (raramente tres) sépalos no gibosos, ni esponjosos y no soldados en la base (*A. lombardoi* tiene cuatro sépalos gibosos, esponjosos y soldados en la base). Por otro lado, *A. deflexus* presenta pericarpio liso con forma elipsoide o piriforme, mientras que *A. macrocarpus* lo tiene reticulado-rugoso en los dos tercios proximales, con forma de botella.

En la diagnosis original de *Amarantellus argentinus*, Spegazzini (1901: 344) no menciona material de herbario y dice: “Frequens ad viarum latera in La Plata, Oct. 1901”. En el herbario LP el ejemplar *Spegazzini s.n.* (LPS12082) tiene una etiqueta agregada en la que escrito en lápiz dice “La Plata, I/1901.”, no habiendo indicios que lleven a pensar

que la misma haya sido escrita por Spegazzini. Además, el LP cuenta con otros tres ejemplares coleccionados por Spegazzini en la ciudad de La Plata cuyas fechas de colección son posteriores a la de la publicación de la descripción de *A. argentinus*. Finalmente, existen en dicho herbario otras dos colecciones de Spegazzini con fecha de 1898 que podrían considerarse como material tipo. No fueron recolectadas en La Plata sino en “La Pantanosa - Río Negro, Carmen de Patagones, Feb. 1898 C. S.” [código de barras LP002713] y en “La Verde punta Rubia, Río Negro, Feb. 1898, C. S.” [código de barras LP002714]. La Pantanosa es una laguna y Punta Rubia una estancia, ambos sitios ubicados en el Pdo. de Patagones (Buenos Aires, Argentina). Los materiales se corresponden con la diagnosis original encontrándose en buen estado de conservación, designándose al ejemplar LP002713 como lectotipo de *A. argentinus* por presentar hojas mejor desarrolladas y numerosas inflorescencias.

Ejemplares examinados. ARGENTINA. **Buenos Aires:** Pdo. Avellaneda, Villa Domínico, *A. Castellanos s.n.* (BA-62952); Pdo. Chacabuco, 24 feb. 1881, *C. L. Spegazzini s.n.* (LP); Chacabuco, Lynch, *C. L. Spegazzini s.n.* (LP); Pdo. Chascomús, Chascomús, Ea. Vitel, feb. 1974, *C. Berg s.n.* (LP); Pdo. de la Costa, Rincón de Viedma, Bahía de Samborombón, *E. J. Ringuelet* 325 p.p. (LP); Grl. Madariaga, Pinamar, *A. L. Cabrera* 10157 (LP); camino a Punta Piedras, *A. L. Cabrera* 1739 (LP); Pdo. Grl. Las Heras, Ea. Sandubehere, *A. P. Rodrigo* 3425 (LP); Pdo. Grl. Villegas, Grl. Villegas, campo de Bunge, *A. L. Cabrera* 5707 (LP); Pdo. Hurlingham, *H. Schwabe* 385 (LP); Pdo. La Plata, La Plata, *N. D. Bayón* 1344 (LPAG); Bosque, *A. L. Cabrera* 5153, 10058 (ambos en LP); La Plata, *H. A. Fabris* 6055 (LP); La Plata, 3 ene. 1973, *Panella s.n.* (LPAG); La Plata, ene. 1902, *C. L. Spegazzini s.n.* (siete ejemplares en LP); La Plata, *N. D. Bayón* 625a (LPAG); Pdo. Lincoln, Lincoln, *N. D. Bayón* 337 (LPAG); Pdo. Lobería, Lobería, feb. 1918, *A. Scala s.n.* (LP); Pdo. Monte Hermoso, Monte Hermoso, 1916, *E. Carette s.n.* (LP); Pdo. Patagones, San Blas, A. Jabalí, 24 dic. 1981, *T. M. Pedersen s.n.* (CTES); Est. Punta Rubia, feb. 1898, *C. Spegazzini s.n.* (LP); Pdo. San Fernando, Isla Martín García, *A. Pastore* 335 bis (LP); Pdo. San Miguel, Villa de Mayo, *J. Brizuela* 1615 (CTES); Pdo. Tigre, Tigre, *Lanfranchi* 521 (LP); Delta, A. Tuyupané, *A. C. Scala* 107 (LP); Delta del Paraná, A. Gálvez, *A. T. Hunziker* 862 (BA); Pdo. Trenque Lauquen, Trenque Lauquen, ene. 1943, *J. Pergolani s.n.* (BA-28171); Pdo. Tres Arroyos, *V. Rodríguez* 478 (CTES); Pdo. Torquinst, Sa. de la Ventana, nov. 1895, *C. L. Spegazzini s.n.* (LP). **Catamarca:** Dep. Paclín, Agua de Mato, 18 ene. 1947, *C. A. O'Donell s.n.* (LIL). **Chubut:** Dep. Sarmiento, Lago Musters, *E. D. M. Kreibohm* 313 (LP). **Córdoba:** Dep. Marcos Juárez, Leones, 17 nov. 1965, *W. Patridge s.n.* (BA-60405); Dep. Pres. R. Sáenz Peña, entre Laguna del Monte y La Cesira, *A. T. Hunziker* 18677 (CORD); Dep. Totoral, entre La Paz y Ascochinga, a 3 km de la última, *A. T. Hunziker* 23561 (CORD). **Entre Ríos:** Dep. Federación, Cnia. Santa Eloisa, *T. M. Pedersen* 8149 (CTES, SI); Dep. Gualeguaychú, ca. Urdinarrain, *T. M. Pedersen* 10289 (CTES); Dep. Nogoyá, Crucecitas, *T. M. Pedersen* 8255

(CTES); Dep. Villaguay, Ruta 18 entre Viale y Villaguay, *N. Troncoso et al.* 2797 (CTES). **Jujuy:** Dep. Tumbaya, Volcán, *Castillón* 58 (LIL); *R. Schreiter* 2576 (LIL). **La Pampa:** Dep. Catriló, Catriló, *J. Fortuna* 15 (LIL); Lonquimay, 15 dic. 1944, *J. Fortuna s.n.* (LIL-148810). **San Juan:** Dto. Jáchal, Bella Vista, El Salto, *R. Kiesling* 6672 (SI). CHILE. **Región del Libertador General Bernardo O'Higgins:** Rancagua, feb.–abr. 1818, *s. coll.* (SGO-048376). **Región Metropolitana de Santiago:** Santiago, *s. coll.* 2395 (SGO-048375).

ESPAÑA. **Canarias:** Pcia. Las Palmas, Isla Lanzarote, Famara, 28 oct. 1974, *A. Hansen s.n.* (CTES).

II. 16. *Amaranthus dinteri* Schinz, Mem. Herb. Boiss. 20: 15. 1900. TIPO: Sudáfrica. Cape: South-West Africa, Salem, 29 jul. 1898, *C. Dinter* 129 (holotipo, Z [código de barras] Z000000244!). Figura 32.

Hierba anual; tallos principales decumbentes, algunas veces erectos, 10–40 cm, ramificados especialmente en la base de los mismos, subglabros o con pelos cortos rectos o papiliformes cuando jóvenes. Hojas con pecíolo de 5–20 mm, glabras o apenas pubescentes, lámina obovada u obovado-elíptica, ondulada, 5–25(–30) × 3–14 mm, atenuada en la base, obtusa en el ápice, redondeada o retusa, a menudo con un mucrón de 0.1–0.5 mm. Inflorescencias axilares, en glomérulos verdosos, 5–8 mm diám, los que se acercan y confluyen hacia el ápice de los tallos; brácteas y bractéolas lanceoladas, 1–2.5 mm, más cortas que los sépalos, membranáceas, con la vena media de color verde y excurrente, curvas y reflejas en el ápice. Flores de ambos sexos sobre una misma inflorescencia. Flores estaminadas con 3 sépalos lanceolados a elípticos, 1–2.2 mm, cortamente acuminados, 3 estambres. Flores pistiladas con 3 sépalos ovados a oblongos, 1.5–3.5 mm, desiguales, con una zona blancuzca y la vena media de color verde, no ramificada, algunas veces conspicuamente reflejos, usualmente agudos en el ápice con un apículo de 0.1–0.5(–0.75) mm; estigmas 3, rectos o apenas reflejos, 0.5–0.75 mm. Frutos dehiscentes, con el opérculo rugoso, urna lisa, más cortos o casi igualando a los sépalos; semillas de color negruzco o castaño, 1.1–1.4 mm diám, brillantes en el área central, semibrillantes y finamente reticuladas en el área marginal.

Distribución y ecología. *Amaranthus dinteri* se distribuye en el Sur y suroeste de África. Ocasionalmente introducida en Europa continental (Alemania, Suecia y Suiza) y una vez hallado en Gran Bretaña (Aellen, 1959; Brenan, 1981). Se ha observado que esta especie es consumida por el ganado lanar (*MacGregor s.n.*, NBG). Florece entre los meses de febrero y mayo.

Discusión. *Amaranthus dinteri* es una especie muy cercana a *A. capensis*, de la que se diferencia por tener sépalos de las flores pistiladas ovados u oblongos, acuminados, no ensanchados distalmente. Por su lado, *A. capensis* tiene los sépalos de las flores pistiladas lanceolados o espatulados, desde obtusos a acuminados, con uno o dos de ellos ensanchados distalmente, mientras que *A. dinteri* cuenta con sépalos de las flores pistiladas ovados u oblongos, agudos, no ensanchados y con un área blancuzca con nervios verdes.

CLAVE PARA LA DIFERENCIACIÓN DE LAS SUBESPECIES DE *AMARANTHUS DINTERI*

1. Entrenudos cortos, aún en los tallos principales, de hasta 7(–10) mm; pecíolo siempre breve, de hasta 7 mm; lámina pequeña, de hasta 8 mm (4 mm de ancho) *A. dinteri* Schinz. subsp. *brevipetiolatus* Brenan
- 1'. Entrenudos de longitud variable, pero aquellos de los tallos principales al menos, comparativamente largos, 10–13 mm; pecíolo variable pero algunos de al menos 15(–20) mm; lámina de 10–25(–30) mm *A. dinteri* Schinz. subsp. *dinteri*

II. 16a. *Amaranthus dinteri* Schinz subsp. ***brevipetiolatus*** Brenan, J. S. African Bot. 47(3): 474. 1981. TIPO: Sudáfrica. Orange: Bloemfontein, 24 ene. 1976, *J. P.M. Brenan* 14095 (holotipo, K [código de barras] K000243578 no visto; isotipos, NBG [cb] NBG0127904-0 no visto, imagen!, PRE [cb] PRE0617572-0 no visto, imagen!).

Amaranthus dinteri subsp. *brevipetiolatus* se caracteriza por sus entrenudos, pecíolos y láminas breves.

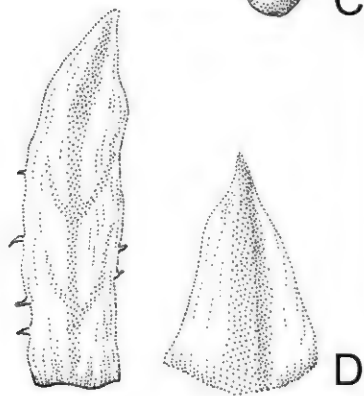
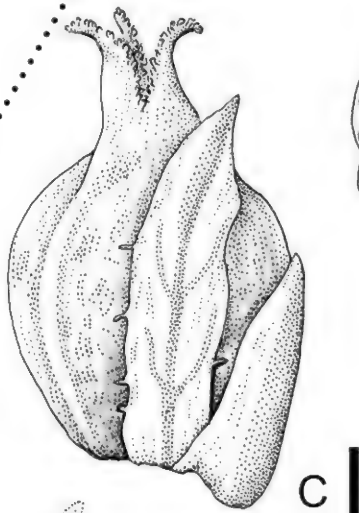
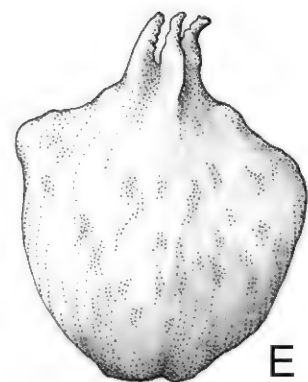
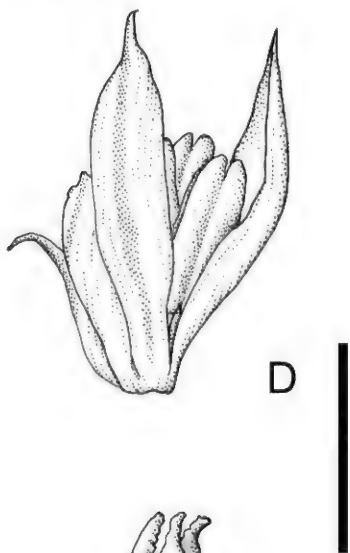
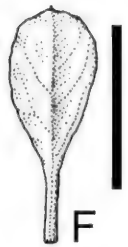
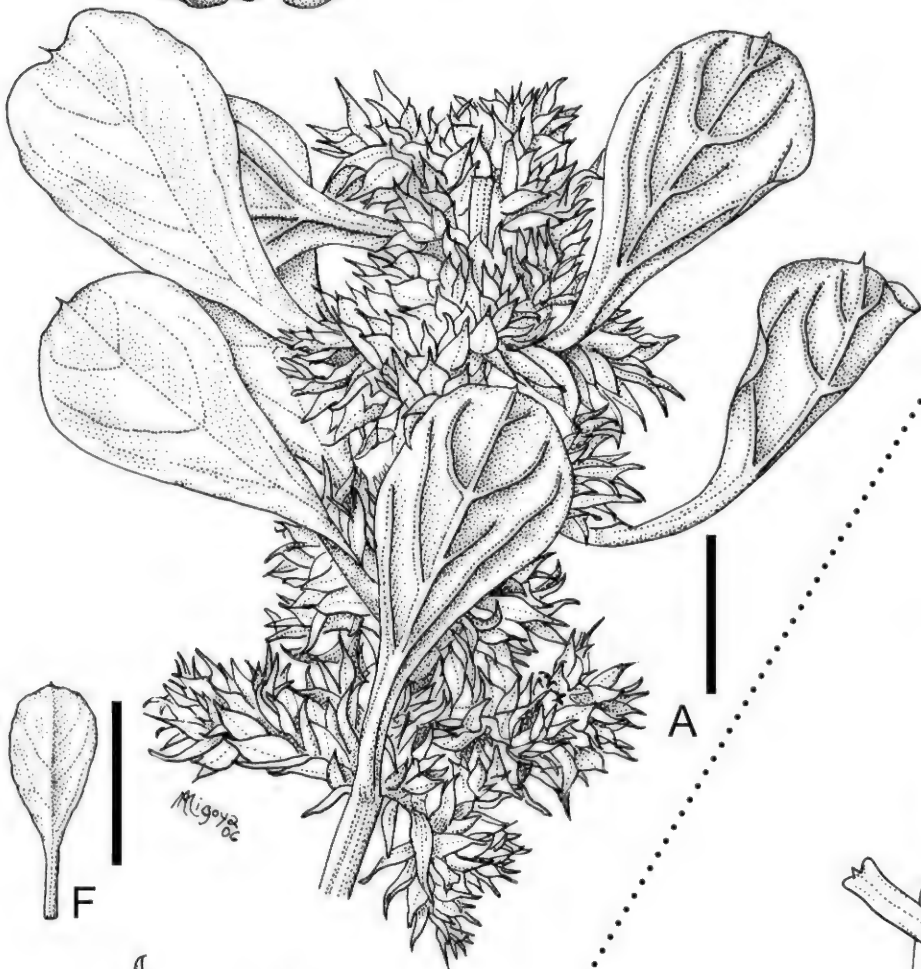
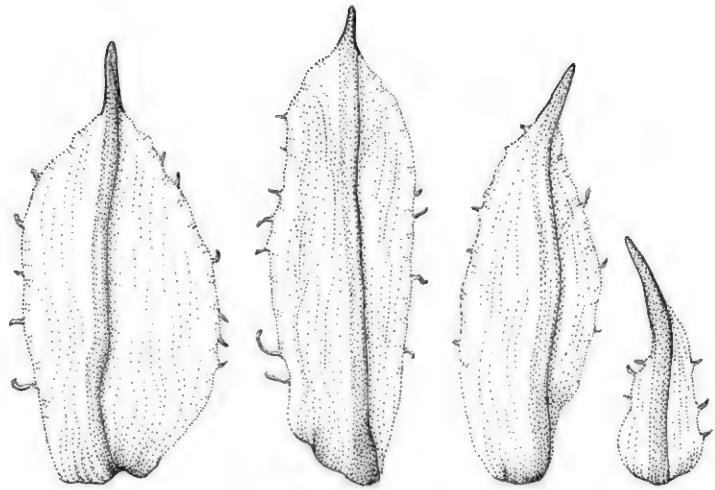
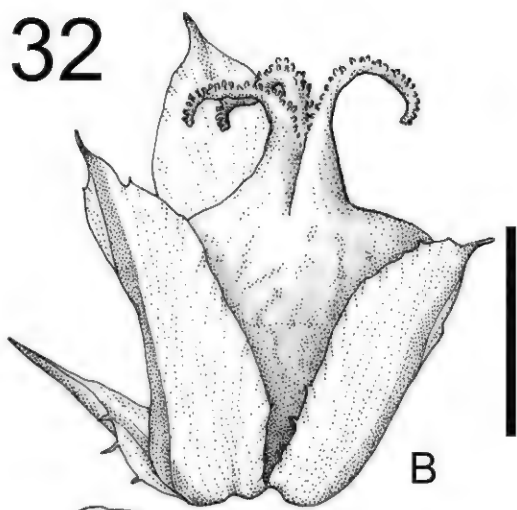
II. 16b. *Amaranthus dinteri* Schinz subsp. ***dinteri***.

Amaranthus dinteri subsp. *dinteri* presenta entrenudos de longitud variable, pero al menos aquellos de los tallos principales son comparativamente más largos que en *A. dinteri* subsp. *brevipetiolatus*, como así también los pecíolos y las láminas.

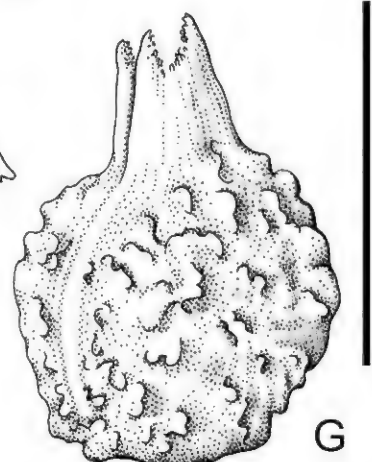
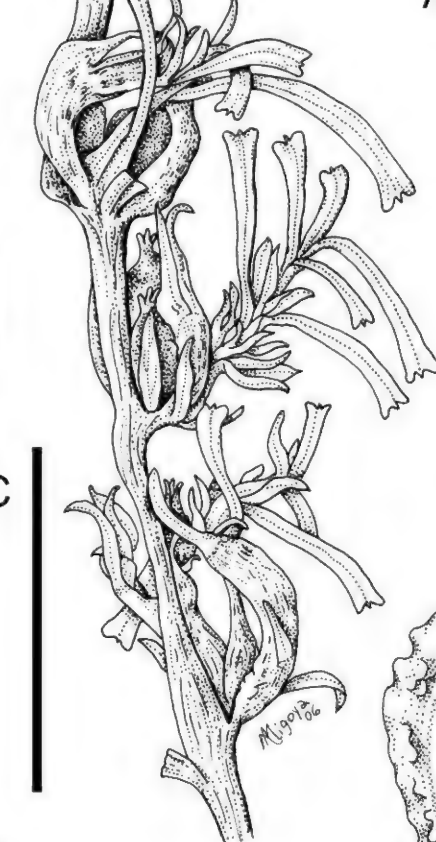
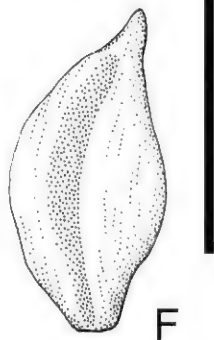
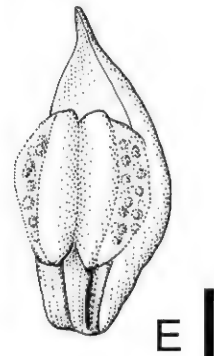
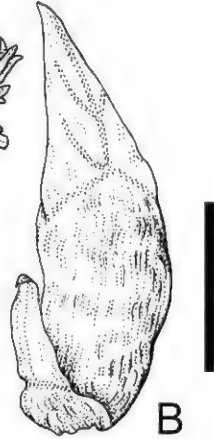
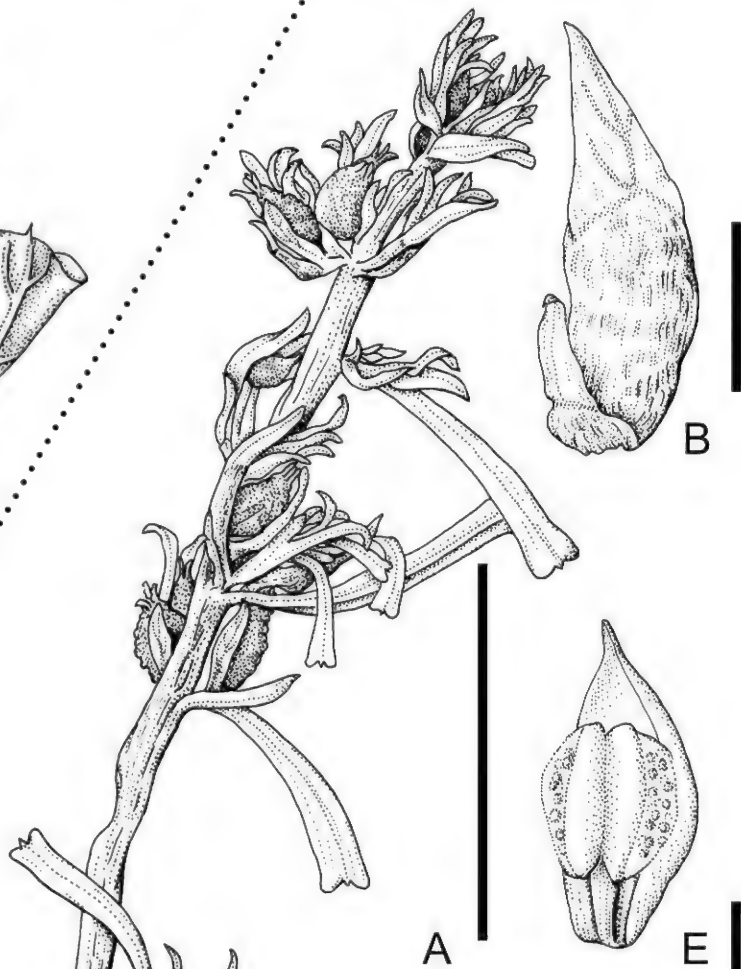
Ejemplares examinados. SUDÁFRICA. **Cape:** SE de Nieuwoudtville, 7 mayo 1986, *N. MacGregor s.n.* (NBG). Steynsburg, Groote Vis. R. sobre la ruta Spitskopvlei-Conway al NE de Graaff-Reinet, *J. P. M. Brenan* 14080 (NBG). **North Cape:** Kimberley, 31 mi. O de Douglas, *R. H. Compton* 23989 (NBG). **West Cape:** Laingsburg, Koup, *R. H. Compton* 10399 (NBG).

II. 17. *Amaranthus furcatus* J. T. Howell, Proc. Calif. Acad. Sci., Ser. 4, 21: 94. 1933. TIPO: Ecuador. Galápagos: Isla Santa Cruz (Indefatigable), Academy Bay, 3 mayo 1932, *J. T. Howell* 9063 (holotipo, CAS [código de barras]

32



33



CAS0000458 no visto, imagen!; isotipos, CORD!, US [cb] US00106244 no visto, imagen!). Figura 33.

Hierba anual; tallos postrados, de hasta de 20 cm, angulosos, glabros. Hojas con pecíolo poco diferenciado, de color verde-grisáceo, glabras, con lámina linear a estrechamente obcordada, decurrente sobre el pecíolo y ensanchándose gradualmente hacia el ápice, no ondulada, $10\text{--}35 \times 0.4\text{--}3$ mm, tendientes a ordenarse en forma dística, atenuadas en la base, bifurcadas en el ápice formando dos lóbulos un tanto divergentes, con un breve mucrón, vena media conspicua a diferencia de las secundarias. Inflorescencia predominantemente en monocasios axilares, con los ejes engrosados hacia la madurez, corchosos, curvados, incluyendo a los frutos; brácteas y bractéolas linear-lanceoladas, o deltoides cuando se disponen sobre los ejes engrosados, de 0.7–1 mm, algo más cortas que los sépalos, membranáceas, con la vena media conspicua, de color verde, ápice agudo o subagudo. Flores de ambos sexos sobre la misma inflorescencia. Flores estaminadas con 1 sépalo ovado, 0.9–1.1 mm, 1 estambre. Flores pistiladas con 1 sépalo linear-oblongo, 0.9–1.3 mm, más corto que los estigmas, o a veces alcanzándolos, con su vena media de color verde, ramificada, con márgenes blanquecinos, agudo; estigmas 3, engrosados en la base, adelgazándose gradualmente. Frutos indehiscentes, comprimidos, rugosos, obovados, castaño oscuros, formando un pico 3-dentado hacia el ápice; semillas de color negro, 0.8–1 mm diám, brillantes, lisas en el área central, punteadas en la marginal, con el margen muy agudo.

Distribución. *Amaranthus furcatus* es un endemismo de las Islas Galápagos que ha podido ser estudiado solo a partir del material tipo y del protólogo. Según Eliasson (1985), podría ser que esta especie esté incluida dentro del rango de variación de *A. sclerantoides*.

Discusión. *Amaranthus furcatus* se asemeja por sus flores a *A. peruvianus* y a *A. sclerantoides*. Se parece a *A. peruvianus* porque esta última tiene generalmente un único sépalo en su flor pistilada y puede mostrar un único estambre en la estaminada, pero sus hojas son muy distintas. Mientras que en *A.*

peruvianus son espatuladas u orbiculares, en *A. furcatus* son lineares o delgadamente obcordadas. Con *A. sclerantoides* comparte la forma linear de las hojas y las semillas con el borde notablemente agudo, aunque se diferencian en el número de estambres y en el de sépalos de las flores de ambos sexos: mientras que *A. sclerantoides* tiene tres o cuatro sépalos y el mismo número de estambres en las flores estaminadas y tres (raro dos) sépalos en las pistiladas, *A. furcatus* tiene un solo sépalo en ambas flores y un solo estambre. Finalmente, al igual que *A. crassipes* se particulariza por el engrosamiento de los ejes de la inflorescencia, como así también el aspecto encorvado de los mismos. Sin embargo, *A. crassipes* tiene cinco sépalos en sus flores pistiladas y sólo dos estigmas.

II. 18. *Amaranthus graecizans* L., Sp. Pl. 2: 990. 1753. *Galliardia graecizans* (L.) Nieuwl., Amer. Midl. Naturalist. 3: 278. 1914, comb. inval. [*Galliardia* Bubani, nom. nud.]. TIPO: Estados Unidos de América. “Habitat in Virginia”, [J.] Clayton 442 (lectotipo, designado por Fernald [1945: 139], tab. 187, BM [código de barras] BM000051563 no visto, imagen!). Figura 34.

Hierba anual; tallos principales erectos, ascendentes o decumbentes, de hasta 45(–70) cm, fuertes o delicados, glabros o apenas pubescentes, especialmente arriba. Hojas con pecíolo de 0.3–2.7 mm, glabras o apenas pubescentes sobre las venas abaxiales primarias y secundarias, lámina elíptico-ovada, rómbica-ovada, ovada, oblonga o linear-lanceolada, no ondulada, $(0.7\text{--})2\text{--}3.5\text{--}(4) \times (0.2)1\text{--}2.5$ cm, atenuada a cuneada en la base, aguda a obtusa en el ápice, a veces retusa, con un mucrón de 0.3 mm. Inflorescencias axilares en glomérulos de 0.5–0.8 mm diám, que se aproximan hacia el ápice de los tallos, formando pseudoespigas foliosas, verdosas; brácteas y bractéolas angostamente ovado-lanceoladas a lanceoladas, 0.7–1.5 mm, apenas más cortas que los sépalos, membranáceas, acuminadas con una pequeña arista formada por la vena media excurrente. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con 3 sépalos lanceolado-oblongos, 1.1–1.3 mm, agudos o algunas veces obtusos, a veces terminados en un apículo de hasta 0.5 mm, membranáceos, 3 estambres. Flores pistiladas con 3 sépalos elípticos a lanceolado-

←
Figura 32. *Amaranthus dinteri* Schinz subsp. *dinteri*. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. *Amaranthus dinteri* subsp. *brevipetiolatus* Brenan. —F. Hoja. A, ilustrado de *Dinter* 129 (Z); B–E, de *Brenan* 14080 (NBG); F, de *Brenan* 14095 (PRE). Las barras de escala para A, F = 5 mm; para B–E = 1 mm.

Figura 33. *Amaranthus furcatus* J. T. Howell. —A. Hábito fértil. —B. Eje engrosado de la inflorescencia. —C. Flor pistilada. —D. Sépalo y bráctea de la flor pistilada. —E. Flor estaminada, vista ventral. —F. Flor estaminada, vista dorsal. —G. Fruto. A–G, ilustrado de *Howell* 9063 (CAS). La barra de escala para A = 5 mm; para B–G = 1 mm.

oblongos, 1.2–1.9 mm, agudos o acuminados, mucronados o aristados dependiendo de las subespecies, con márgenes membranáceos, herbáceos en las proximidades de la vena media; estigmas 2 o 3, delgados, flexuosos, 0.3–0.5 mm. Frutos por lo general dehiscentes, algunas veces indehiscentes, con un rostro corto y liso, con el cuerpo más largo que los sépalos, pericarpo usualmente arrugado, pocas veces liso; semillas de color negro, 1.2–1.5 mm diám, brillantes en el área central, reticuladas y opacas en el área marginal.

CLAVE PARA LA DIFERENCIACIÓN DE SUBESPECIES DE
AMARANTHUS GRAECIZANS

- 1. Sépalos con aristas de 0.3–0.75 mm, frecuentemente divergentes 2
- 1'. Sépalos con mucrón de hasta 0.25 mm, usualmente rectos 3
- 2(1). Frutos dehiscentes *A. graecizans* L. subsp. *thellungianus* (Nevski ex Vassilez.) Gusev
- 2'. Frutos indehiscentes *A. graecizans* L. subsp. *aschersonianus* (Thell.) Costea, D. M. Brenner & Tardif
- 3(1'). Láminas foliares de los tallos principales lineal-lanceoladas u oblongas, cuya longitud supera en más de 2.5 veces el ancho
..... *A. graecizans* L. subsp. *graecizans*
- 3'. Láminas foliares de los tallos principales ampliamente ovadas, rómbico-ovadas o elíptico-ovadas, cuya longitud es inferior a 2.5 veces el ancho
.... *A. graecizans* subsp. *sylvestris* (Villiers) Brenan

II. 18a. *Amaranthus graecizans* L. subsp. *aschersonianus* (Thell.) Costea, D. M. Brenner & Tardif, Econ. Bot. 57(4): 646. 2003. Basónimo: *Amaranthus aschersonianus* Thell., Syn. Mitteleur. Fl. 5 (Abth. 1): 309. 1919. *Amaranthus roxburghianus* Nevski var. *aschersonianus* (Thell.) N. C. Nair, J. Bombay Nat. Hist. Soc. 73(1): 61. 1976. TIPO: Sudán. Ad pagum Cordofanum Abu-Gerad, 22 sep. 1839, K. *Kotschy 48* (lectotipo, aquí designado, S-07-12119 no visto, imagen!; isolectotipos, BR p.p. [ejemplar de la izquierda] [código de barras] BR00000881927 no visto, imagen!, BR [cb]

BR0000008819468 no visto, imagen!, K [cb]
K000243574 no visto, imagen!).

Amaranthus polygamus auct. non Linn.

Amaranthus graecizans subsp. *aschersonianus* se caracteriza por poseer sépalos aristados, con aristas divergentes y frutos indehiscentes.

Distribución. *Amaranthus graecizans* subsp. *aschersonianus* se encuentra en África tropical (Sudán) e India. Florece y fructifica en septiembre.

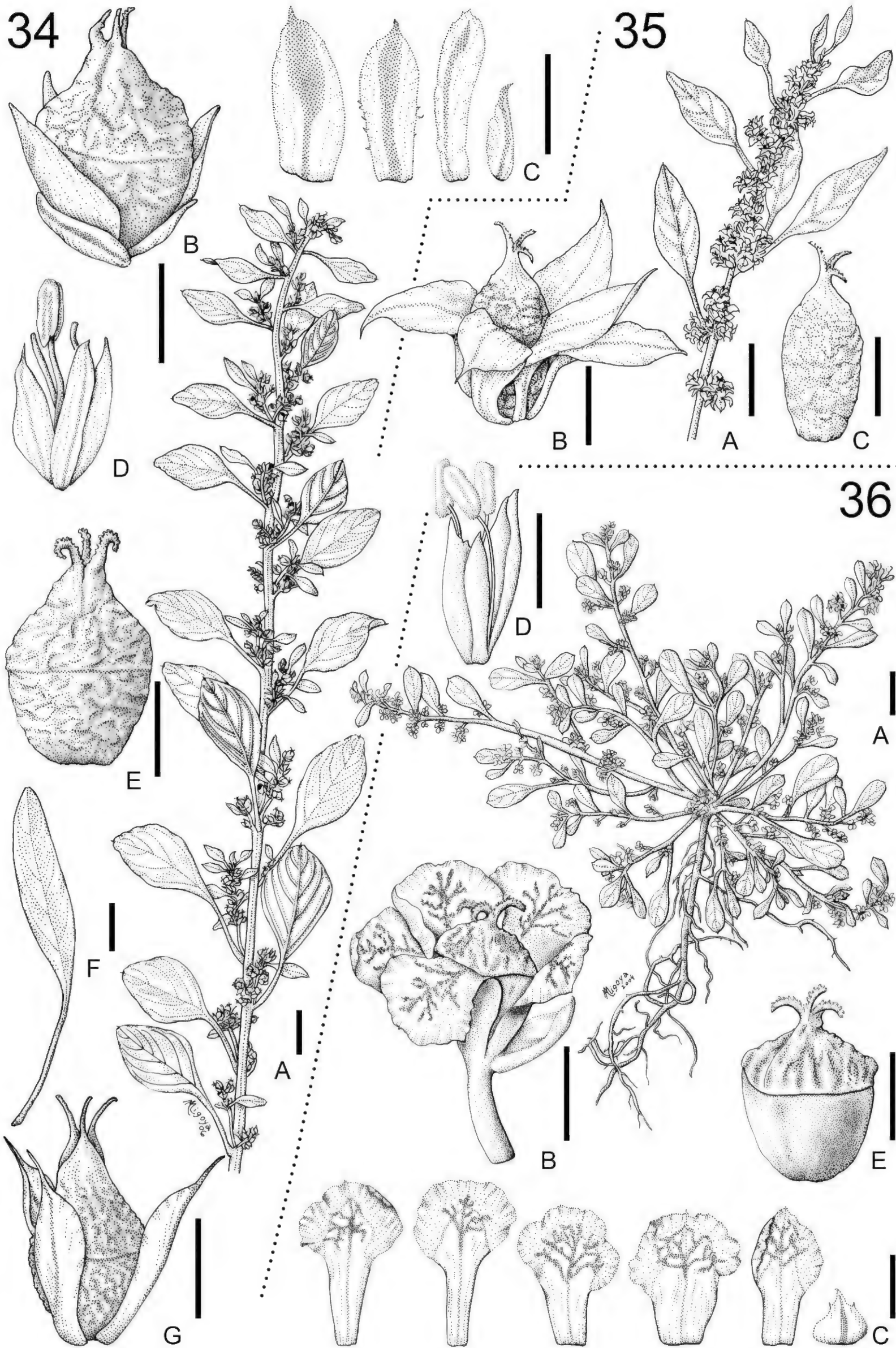
Discusión. En la diagnosis original de *Amaranthus aschersonianus*, Thellung (1919a: 309) menciona a los sintipos *Kotschy 48* y *Kotschy 82*. Del primero existen cuatro isosintipos, dos de ellos depositados en BR, y los otros dos en K y S. Del segundo se han hallado tres isosintipos depositados en BR, K y S. Todos ellos se encuentran en buen estado de conservación, y sobre imágenes muy detalladas se pueden apreciar las aristas de las brácteas, bractéolas florales y de los sépalos, como así también que los frutos son indehiscentes. El ejemplar S-07-12119 es seleccionado como lectotipo pues cuenta con tres fragmentos de plantas con numerosas hojas, flores y frutos que se corresponden con el protólogo.

Costea et al. (2003c) al estudiar un material proveniente de la India, realizan una nueva combinación basándose en *Amaranthus angustifolius* Lam. var. *aschersonianus* Thell.: *A. graecizans* L. subsp. *aschersonianus* (Thell.) Costea, D. M. Brenner & Tardif. Consideran que la subespecie más cercana es *A. graecizans* subsp. *thellungianus* centrando su semejanza en las brácteas, bractéolas y tépalos con aristas (no mucrones) de hasta 0.7 mm. Por otra parte, establecen como diferencias los dos siguientes caracteres propios de *A. graecizans* subsp. *aschersonianus*: 1) el primero se refiere a las cimas de las plantas adultas, usualmente aglomeradas en inflorescencias axilares pero también en densas, gruesas y breves inflorescencias terminales, y 2) frutos indehiscentes. Se desprende

Figura 34. *Amaranthus graecizans* L. subsp. *sylvestris* (Vill.) Brenan. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. *Amaranthus graecizans* subsp. *graecizans*. —F. Hoja. *Amaranthus graecizans* subsp. *thellungianus* (Nevsky) Gusev. —G. Flor pistilada. A–E, ilustrado de Popov & Vvedensky 423 (BA); F, de Herb. Linnaeus 1117.3 (LINN); G, redibujado de Townsend (1974a). Las barras de escala para A, F = 1 cm; para B–E, G = 1 mm.

Figura 35. *Amaranthus grandiflorus* (J. M. Black) J. M. Black. —A. Hábito fértil. —B. Flor pistilada. —C. Fruto. A, adaptado y redibujado de la Flora de South Australia (<www.flora.sa.gov.au>). B, C, redibujado de <http://plantnet.rbgsyd.nsw.gov.au>. La barra de escala para A = 1 cm; para B, C = 2 mm.

Figura 36. *Amaranthus hunzikeri* N. Bayón. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A–E, ilustrado de holotipo *Reca & Ramadori 17* (SI). La barra de escala para A = 1 cm; para B–E = 1 mm. Adaptado y rediseñado desde *Novon* 17(3): 295, fig. 1. 2010.



que el carácter de las inflorescencias terminales no es constante, al afirmar que usualmente son axilares. De su publicación surge que no tuvieron acceso al material tipo, indicando solamente que se trata de un ejemplar de Sudán.

En las imágenes del material tipo es posible observar que las inflorescencias son axilares (no terminales), que los sépalos de las flores pistiladas son aristados y que los frutos son indehiscuentes. Al no presentarse inflorescencias terminales, queda como único carácter que permite distinguir a las dos subespecies la dehiscencia de los frutos, por lo que finalmente en base al mismo, se decide reconocer como taxonómicamente distinto al taxón *Amaranthus graecizans* subsp. *aschersonianus*.

Ejemplar examinado. SUDÁN. Ad pagum Cordofanum Abu-Gerad, 30 sep. 1840, K. Kotschy 82 (sintipo, *Amaranthus graecizans* subsp. *aschersonianus*, BR [código de barras] BR0000006278960 no visto, K-243572 no visto, imagen!, S-07-12118 no visto, imagen!).

II. 18b. *Amaranthus graecizans* L. subsp. *graecizans*.

Amaranthus angustifolius Lam., Encycl. Méth. 1: 115. 1783, nom. illeg.

Amaranthus graecizans subsp. *graecizans* se caracteriza por sus hojas linear-lanceoladas u oblongas y sépalos mucronados.

Distribución y ecología. *Amaranthus graecizans* subsp. *graecizans* es nativa de la región del Mediterráneo, África tropical y Asia occidental. Parece ser la forma dominante en las zonas más cálidas de Europa y suroeste de Asia (Arabia Saudita, Irak, sur de Irán y Jordania). En África se la halla en el oeste, área tropical del noreste y en el sur. En tierras bajo riego se transforma en maleza (Aellen, 1972; Carretero, 1990).

Nombre vulgar. Mediterranean amaranth (Mosyakin & Robertson, 2003).

Discusión. *Amaranthus graecizans* subsp. *graecizans* suele ser confundida con *A. blitoides*, seguramente por las hojas linear-lanceoladas u oblongas, sus flores reunidas en glomérulos axilares y sus frutos dehiscentes. No obstante, *A. graecizans* subsp. *graecizans* tiene invariablemente tres sépalos en sus flores pistiladas, mientras que *A. blitoides* tiene por lo general cinco sépalos, aunque también rara vez puede tener tres o cuatro.

Amaranthus angustifolius Lam. se trata de un nombre ilegítimo, siendo un nombre superfluo que aparece como sinónimo de *A. graecizans* (Art. 52.2, McNeill et al., 2012).

Según Fernald (1945) Linneo se basó en el material de Clayton al describir esta especie. En Fernándes y Barros Neves (1957), Dandy y Melderis cuestionan la elección del lectotipo por parte de Fernald, porque consideran que se debió haber tenido en cuenta al ejemplar del *Herb. Linnaeus 1117.3* (LINN no visto, imagen!) que concuerda con las características de la especie (cf. Jarvis, 2007). Se acepta la propuesta efectuada por Fernald dado que por un lado antecede a la de Dandy y Melderis, y por el otro se observa que el ejemplar de Clayton posee mayor abundancia de órganos reproductivos.

II. 18c. *Amaranthus graecizans* L. subsp. *sylvestris* (Vill.) Brenan, Watsonia 4: 273. 1961. Basónimo: *Amaranthus sylvestris* Vill., Cat. Jard. Pl. Strasbourg: 111. 1807. *Amaranthus graecizans* L. var. *sylvestris* (Vill.) Asch. & Schweinf., Beitrege zur Flora Aethiopiens: 176. 1867. TIPO: *Herb. Tournefort 1849* (lectotipo, designado por Townsend [1985: 31], P no visto).

Amaranthus graecizans subsp. *sylvestris* se reconoce por sus hojas anchamente ovadas, rómbico-ovadas o elíptico-ovadas y sépalos mucronados.

Distribución y ecología. *Amaranthus graecizans* subsp. *sylvestris* es la subespecie más común de Europa, aunque se halla presente también en el Cáucaso, Palestina (Zohary & Feinbrun-Dothan, 1966), Irán, Afganistán (Aellen, 1972), Pakistán y noroeste de India (Townsend, 1974a), y este del continente africano. Esta subespecie ha sido hallada también en América del Norte (Mosyakin & Robertson, 2003), comúnmente como maleza de lugares cultivados o cercanos a ciudades, en bordes de bosques, pastizales o cerros rocosos de poca altura, entre los 450 m y 550 m. Florece entre los meses de julio y octubre.

Ejemplares examinados. ESPAÑA. **Canarias:** Las Palmas, 23 jun. 1912, s. coll. (LP). **Cataluña:** Barcelona, Vich, Gonzalo 4634 (SI); Barcelona, Manlleu y S. Hipólito, Gonzalo 5542 (SI); Barcelona, Manlleu, Gonzalo 6892, 6893, 6894, 6895 (los cuatro en SI); Barcelona, Gavá, F. Sennen 3564 (SI). FRANCIA. Córcega, Ueimberg, P. Aellen 152 (LP). REPÚBLICA CHECA. Bohemia centralis, Praha-Troja, oct. 1937, M. Deyl s.n. (BA 22195).

UZBEKISTÁN. Tian Shan occidentalis, Tasch Kent, M. G. Popov & A. I. Vvedensky 423 (BA).

II. 18d. *Amaranthus graecizans* L. subsp. *thellungianus* (Nevski ex Vassilcz.) Gusev, Bot. Zhurn. (Moscú & Leningrado) 57(5): 462. 1972. Basónimo: *Amaranthus thellungianus* Nevski ex Vassilcz., Acta. Inst. Bot. Acad. Sc. URSS, 1(4): 311. 1937. TIPO: Turkmenistán. "In

angustiis Bulak-Dara ad pedem montium Kuitang supra pagum Karluk, 11 jul. [sine anno]”, S. A. Nevsky 730 (holotipo, LE no visto; fotografía del isotipo, K [código de barras] K000814926 no visto, imagen!).

Amaranthus blitum L. var. *polygonoides* Moq. in de Candolle, Prodr. 13(2): 263. 1849. *Amaranthus angustifolius* Lam. var. *polygonoides* Thell., Syn. Mitteleur. Fl. 5 (Abth. 1): 308. 1919. *Amaranthus roxburghianus* H. W. Kung, Fl. Illust. N. China 4: 19. 1935. TIPO: India. Trichinopoly, 8 nov. 1826, N. Wallich 6906 (holotipo, K [código de barras] K000195197 no visto, imagen!).

Amaranthus thunbergii Moq. var. *grandifolius* Suess., Mitt. Bot. Staats. München 1: 73. 1951. TIPO: Tanzania. Lushoto. Amani, jun. 1943, P. G. Greenway AN1294 (holotipo, EA [código de barras] EA000001816 no visto, imagen!; isotipo, PRE [cb] PRE0775684-0 no visto, imagen!).

Amaranthus graecizans L. subsp. *thellungianus* se caracteriza por contar con sépalos aristados y frutos dehiscentes.

Distribución. *Amaranthus graecizans* subsp. *thellungianus* crece en pastizales de India, sur de África (Tanzania), Turkmenistán y Sri Lanka.

Usos. Hortaliza.

Discusión. Cuando Kung (1935: 19) trata *Amaranthus roxburghianus* lo sinonimiza con “*A. acutifolius* Lam. subsp. *polygonoides* (Roxb.) Thell. in Asch. & Gräbner, Syn. Mitteleur. Fl.”, escribiendo erróneamente el epíteto específico (*acutifolius*, sic, en lugar de *angustifolius*). No cabe duda que se está refiriendo a este taxón subespecífico al mencionar en la descripción que los sépalos son acuminados, terminados en una punta aguda, lo que se ve claramente en la ilustración (tab. VIII en Kung, 1935).

Ejemplar examinado. SRI LANKA. Ruhuna Nat. Park, entre Andunoruwa Wewa y Komawa Wewa, R. G. Cooray 70032519R (US).

II. 19. *Amaranthus grandiflorus* (J. M. Black) J. M. Black, Trans. & Proc. Roy. Soc. S. Austr. 60: 166. 1936. Basónimo: *Amaranthus mitchellii* Benth. var. *grandiflorus* J. M. Black, Trans. & Proc. Roy. Soc. S. Austr. 47: 368. 1923. TIPO: Australia. South Australia: Depot Creek, 10 jun. 1883, Herb. R. Tate s.n. (holotipo, AD-99436234 no visto). Figura 35.

Hierba anual; tallos principales erectos, rígidos, 15–40 cm, ramificados, glabros. Hojas pecioladas, lámina ovado-lanceolada a elíptico-lanceolada, algo ondulada, 2–3(–6) cm. Inflorescencias en glomérulos axilares densos, ca. 8–15 mm diám, mayores hacia la base de la planta; brácteas y bractéolas delgadas, 2–3 mm, agudas, acuminadas. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con 5 sépalos lanceolados, 2–2.5 mm, no unguiculados, 3 estambres. Flores pistiladas con 5 sépalos ovado-oblongos a espatulados, de 4–8 mm, los externos casi ovados, brevemente unguiculados, escariosos, con la vena media verdosa, mucronados; estigmas 3. Frutos indehiscentes, (2–)3–5 mm, elipsoides, transversalmente rugosos, angostamente ovados, algo más cortos que el cáliz; semillas negras, 2 mm diám, brillantes.

Distribución y ecología. *Amaranthus grandiflorus* crece al Sur del Northern Territory, en las cercanías del Lago Eyre, en algunas áreas del Southern Territory, al Sudoeste de Queensland, en el Oeste de New South Wales y en los lagos Hattah al Noroeste de Victoria. Crece principalmente en áreas secas, en especial de arenas rojizas (distribución y hábitat tomados de Palmer, 2009).

Discusión. Para Black (1923, 1936), quien crea en primera instancia la variedad y luego le brinda categoría específica a *Amaranthus grandiflorus*, esta especie difiere de *A. mitchellii* en: 1) los sépalos de las flores femeninas que duplican en longitud a los de *A. mitchellii*, contando con una uña corta y lámina ovado-oblonga, en lugar de la uña tan larga como la lámina flabelada de *A. mitchellii*; 2) sus glomérulos son más grandes y más densos que en *A. mitchellii*; 3) los frutos cuentan con surcos transversales y no verticales como en *A. mitchellii*; 4) las semillas son más grandes (2 mm contra 1.5 mm que tienen las de *A. mitchellii*).

Si bien no me ha sido posible observar el material tipo de esta especie, queda claro según la descripción original que se distingue de *Amaranthus mitchellii* por tener los sépalos de las flores pistiladas más grandes, a lo que alude el epíteto específico, como también presenta glomérulos de mayor tamaño.

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II. 20. *Amaranthus hunzikeri* N. Bayón, Novon 17(3): 294–297, fig. 1. 2007. TIPO: Argentina. Catamarca. Laguna Blanca, 14 mar. 1989, 3200–3300 m, A. R. Reca & D. E. Ramadori 17 (holotipo, SI!). Figura 36.

Hierbas anuales; tallos principales postrados o ascendentes 3–14 cm, ramificados en la base, no así en la parte distal, delgados, glabros. Hojas con pecíolo de 4–11 mm, glabras, lámina generalmente espatulada, a veces elíptica u oblonga, no ondulada, 10–17 × 3–9 mm, atenuada o cuneada en la base, redondeada o apenas emarginada en el ápice, de

color verde claro, con un mucrón de 0.5–1 mm. Inflorescencias axilares, en glomérulos redondeados, de hasta 7 mm diám, verdosos o blanquecinos, los que a veces se reúnen en una pseudoespiga breve, de hasta 2 cm, apretada, foliosa, originada en la brevedad de los entrenudos apicales; brácteas y bractéolas deltoides, ovadas, elípticas hasta orbiculares, 0.9–1.3 mm, más cortas que los sépalos, blanquecinas, escarioso-membranáceas, con la vena media de color verde, mucrón 0.2–0.3 mm. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con (2)3 a 5 sépalos oblongos, ovados a elípticos, 1.3–2 mm, subagudos a obtusos, escariosos, con la vena media de color verde, estambres (2)3 o 4. Flores pistiladas con 5 sépalos ampliamente espatulados, 1.7–2.5 mm, con la lámina de 1.4–2.5 mm de ancho, redondeada, adelgazados en una uña de 0.2–0.6 mm de ancho, esponjosos en la base, doblados hacia fuera; flores más anchas que largas; estigmas tres, 0.12–0.40 mm, delgados. Frutos dehiscentes, con el opérculo rugoso, presentando costillas curvas, más cortos que los sépalos, urna lisa; semillas de color castaño-rojizo a negruzco, 0.9–1.3 × 0.5–0.55 mm, lisas y brillantes en el área central, finamente punteadas y opacas en el área marginal.

Distribución y ecología. *Amaranthus hunzikeri* crece en el noroeste de Argentina (Catamarca y Jujuy), en vegas y costado de rutas (Bayón & Vera Bahima 1456, LPAG; Reca & Ramadori 17, SI) entre los 2700 m y los 3600 m. Florece y fructifica en los meses de febrero y marzo.

Discusión. *Amaranthus hunzikeri* es cercana a todas aquellas especies que tienen cáliz con la base de los sépalos ancha y engrosada, esto es *A. anderssonii*, *A. kloosianus*, *A. polygonoides*, *A. squamulatus* y *A. urceolatus*. Todas ellas presentan frutos indehiscentes, salvo *A. squamulatus* que puede tener en algunos casos frutos dehiscentes. De esta última se puede diferenciar porque *A. squamulatus* tiene tallos erectos, hojas no espatuladas y un número constante de cinco sépalos y tres estambres en sus flores estaminadas.

Ejemplares examinados. ARGENTINA. **Catamarca:** Dep. Belén, Laguna Blanca, N. D. Bayón & J. Vera Bahima 1456, 1457, 1462, 1463 (los cuatro en LPAG); Cta. de Randolpho, entre Barranca Larga y Laguna Blanca, N. D. Bayón & J. Vera Bahima 1485 (LPAG); Nacimientos de San Antonio, A. L. Cabrera et al. 32442 (CTES). **Jujuy:** Dep. Tumbaya, Purmamarca, Qda. de Huachichocana, A. L. Cabrera et al. 15036 (LP); Dep. Tumbaya, El Angosto de San José del Chañi, A. L. Cabrera et al. 22451 (LP); Dep. Susques, Susques, 5 mar. 1927, A. Castellanos s.n. (paratipo, *Amaranthus hunzikeri*, BA).

II. 21. *Amaranthus induratus* C. A. Gardner ex J. Palmer & Mowatt, Nuytsia 19(1): 117. 2009. TIPO: 43 mi. S of Derby at river crossing, Western Australia, 25 ene. 1971, K. M. Allan 587 (holotipo, PERTH no visto, imagen!; isotipo, CAMB no visto).

Hierba anual; tallos principales erectos, de hasta 90 cm, redondeados, escasamente pubescentes con pelos glandulares, o volviéndose glabros. Hojas con pecíolo de hasta 25 mm, con lámina linear a angostamente oblonga o angostamente ovada, 15–70 × 2–10 mm, obtusa o emarginada en el ápice, mucronada. Inflorescencias axilares y terminales, las primeras en glomérulos globosos y las segundas en espigas erectas, densas o interrumpidas de hasta 23 cm, algunas veces formando panojas; brácteas y bractéolas ovadas, ca. 1 mm, más breves que los sépalos, agudas en el ápice. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con 5 sépalos angostamente elípticos a obovados, ca. 1.5 mm, obtusos, con el margen membranáceo, blanquecinos, glabros, con la vena media delgada, de color verde, 3 estambres. Flores pistiladas con 5 sépalos obovado-espatulados, 1.5–2.4 mm, obtusos, erectos o recurvos, margen entero, membranáceos, blanquecinos, glabros o glabrescentes, con la vena media ancha, 0.5–1 mm, de color verde, mucronulados; al momento de la fructificación se vuelven más elongados, de hasta 3.5 mm, obovado-espatulados o angostamente obovado-espatulados, endurecidos, de color verde o pajizo, con los márgenes desarrollando una o varias proyecciones a modo de dientes a cada lado en la mitad inferior. Frutos indehiscentes, elipsoides, 1.5–3 mm, algo más cortos que los sépalos, lisos o rugosos, con costillas; las costillas apenas elevadas, rectas, longitudinales, tuberculadas; semillas obovoides, 1.3–1.5 mm, lisas, de color negro-rojizas, brillantes.

Distribución y ecología. *Amaranthus induratus* está presente en Western Australia, en las regiones de Kimberley y de Pilbara. También citado para Northern Territory. Crece en arcillas rojas y suelos cercanos a los cursos de agua o cerca de depresiones arcillosas (distribución y hábitat tomados de Palmer, 2009).

II. 22. *Amaranthus interruptus* R. Br., Prodr. Fl. Nov. Holland. 414. 1810. *Euxolus interruptus* (R. Br.) Moq. in de Candolle, Prodr. 13(2): 267, 275. 1849. TIPO: Australia. Áreas tropicales de Northern Territory y Queensland, “North Coast”, mayo 1802, R. Brown [Iter Australiense]

3048 (holotipo, BM [código de barras] BM000847081 no visto, imagen!). Figura 37.

Amaranthus lineatus R. Br., Prodr. Fl. Nov. Holland. 414. 1810. *Euxolus lineatus* (R. Br.) Moq. in de Candolle, Prodr. 13(2): 267, 276. 1849. TIPO: Australia. Áreas tropicales de Northern Territory y Queensland, “North Coast”, mayo 1802, R. Brown [Iter Australiense] 3049 (holotipo, BM [código de barras] BM000884578 no visto, imagen!).

Hierbas anuales; tallos principales erectos, a veces decumbentes, 15–60 cm, glabros. Hojas con pecíolo de 3–8 mm, glabras, lámina ovada, oblonga o rómbica, no ondulada, $1.2\text{--}5 \times 0.5\text{--}1$ cm, obtusa en el ápice, con un mucrón de 0.3 mm, con el margen ondulado, venas blanquecinas y marcadas en el envés. Inflorescencias terminales y axilares, las primeras en espigas largas y delgadas, de hasta 10 cm, laxas y foliosas en la base, en las que se puede ver el eje, simples o con muy pocas ramificaciones; las segundas en glomérulos axilares densos o laxos, 6–8 mm diám; brácteas y bractéolas ovadas u oblongas, 0.75–1.25 mm, membranáceas, con la vena media de color verde, más cortas que el cáliz. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con 3 a 5 sépalos finamente obovado-oblongos u oblongo-lanceolados, 1.2–1.5 mm, agudos u obtusos, con la vena media marcada, mucronados a cortamente aristados, 3(4) estambres. Flores pistiladas con 5 sépalos angostamente espatulados, 1.4–1.7 mm, agudos a obtusos, mucrón o arista corta de 0.4 mm; estigmas tres, 0.3–0.4 mm, muy delgados. Frutos indehiscentes, con el pericarpio rugoso y membranáceo, de color castaño-verdoso oscuro, salvo en la región próxima a los estigmas en donde se vuelve más claro, tan largo como los sépalos; semillas de color castaño-negruzco, 1 mm diám, muy brillantes en el área central, no así en el área marginal.

Distribución y ecología. *Amaranthus interruptus* es propio de Australia, de la Región de Kimberley de Western Australia (Kununurra, Río Ord y Parque Nacional Bungle Bungle) y también de los arrecifes Ashmore en el Mar de Timor (Western Australia). A su vez, se la puede encontrar en la Meseta de Barkly en el Northern Territory y hacia el Este en Queensland, así como en los Montes Musgrave y Flinders de South Australia (distribución tomada de Palmer, 2009). Florece entre los meses de mayo y octubre.

Discusión. Los frutos indehiscentes y rugosos de *Amaranthus interruptus* recuerdan a los de *A. blitum* y *A. viridis* como ya hiciera notar Bentham (1870). Sin embargo, *A. interruptus* tiene cinco sépalos en sus

flores pistiladas y no dos o tres como en *A. blitum* y *A. viridis*.

Ejemplares examinados. AUSTRALIA. **Northern Territory:** 21 km al SO de Calvert Hills sobre la ruta hacia Cresswell Downs, S. Jacobs 1603 (NSW). **Queensland:** 43 km al O de Emerald sobre Alpha rd., S. Jacobs 346 (NSW). **Western Australia:** East Indian Ocean, West Island, Ashmore Reef, K. F. Kenneally 6359 (CTES); Ashmore Reef, Timor Sea, Middle Island, J. Hicks 83 (CTES).

II. 23. *Amaranthus kloosianus* Hunz., Bol. Soc. Argent. Bot. 4(1–2): 138. 1951. TIPO: Argentina. Salta: Dep. La Viña, La Viña, 1100 m, 18 mar. 1943, A. T. Hunziker 2826 (holotipo, CORD!; isotipos, K, SI no vistos). Figura 38.

Hierba anual; tallos principales erectos, 40–60 cm, ramificados, glabros en la base, escasamente pubescentes cerca de la inflorescencia. Hojas con pecíolo de 2–10 mm, glabras, lámina lanceolada a ovado-lanceolada, no ondulada, $10\text{--}30 \times 3\text{--}8$ mm, atenuada a cuneada en la base, estrechándose gradualmente hacia el ápice, éste redondeado, algunas veces apenas emarginado, con un mucrón de 0.3–0.6 mm. Inflorescencias axilares, en glomérulos de 0.5 cm diám, aunque a veces tendiendo a reunirse en el ápice 2–3 glomérulos, formando una pseudoespiga de 4×0.5 cm; brácteas y bractéolas ovadas a elípticas, 0.7–1.5 mm, más cortas que los sépalos, membranáceas, con la vena media de color verde, conspicua, cortamente mucronadas. Flores de ambos sexos sobre una misma inflorescencia. Flores estaminadas con 5 sépalos obovados a anchamente oblongos, obtusos, redondeados o emarginados, escariosos, con vena media de color verde, 5 estambres. Flores pistiladas urceoladas, con 5 sépalos espatulados, 1.3–2 mm, con la mitad o el tercio superior reflejo, no superpuestos, expandidos, obtusos, redondeados a emarginados en el ápice, vena media engrosada y usualmente ramificada; fusionados y algo más gruesos en la base en un tramo de 0.3–0.6 mm, diámetro floral en la base 1–1.5 mm, adelgazándose en la parte media, permitiendo ver el ovario entre ellos; diámetro del cáliz expandido en la porción distal 1.5–2.5 mm, apenas más corto o más largo que el fruto; estigmas 2, ensanchados en la base, 0.3 mm. Frutos indehiscentes, rugoso-verrucosos, con la base encerrada dentro del tubo del cáliz; semillas de color negro, $0.8\text{--}1 \times 1\text{--}1.1$ mm, brillantes en el centro y castaño y reticuladas en el margen.

Distribución y ecología. *Amaranthus kloosianus* es endémica de las provincias del centro y noroeste de Argentina (Catamarca, Córdoba, Jujuy, La Rioja, Mendoza, Salta y San Luis). Se la suele encontrar en



terrenos llanos del monte, al costado de los caminos y a veces se presenta como maleza poco abundante (*Biurrum* & Blanco 7480, CTES) y crece entre los 350 m y los 2400 m. Florece entre los meses de enero y mayo.

Discusión. *Amaranthus kloosianus* se asemeja a aquellas otras especies que presentan sépalos de las flores pistiladas esponjosos en la base, constituyendo un órgano que hace las veces de flotador para los frutos, facilitando así su dispersión. Este grupo está comprendido por: *A. anderssonii*, *A. hunzikeri*, *A. pedersenianus*, *A. polygonoides*, *A. squamulatus* y *A. urceolatus*. De *A. hunzikeri* y *A. pedersenianus* se diferencia porque estas últimas especies tienen frutos dehiscentes y flores estaminadas con tres a cinco estambres (raramente dos) (no frutos indehiscentes y cinco estambres como *A. kloosianus*). De *A. squamulatus* se diferencia por el hecho de que esta especie tiene un diámetro distal de sus flores pistiladas de 3.5–5 mm y tres estambres (*A. kloosianus* llega a tener un diámetro de 2.5 mm y presenta cinco estambres). De las otras tres se distingue porque *A. urceolatus* tiene tres estambres (rara vez dos), *A. anderssonii* y *A. polygonoides* tienen dos, mientras que *A. kloosianus* tiene cinco.

Ejemplares examinados. ARGENTINA. **Catamarca:** Dep. La Paz, Río de la Dorada, *A. Brizuela* 954, 954 dupl. p.p. (ambos en CTES). **Córdoba:** Dep. San Alberto, entre Villa Dolores y Altautina, *A. T. Hunziker* 9511 (CORD); entre El Chocolate y Estancia Chúa, camino a Chancaní, *A. T. Hunziker* 11515 (CORD). **Jujuy:** Dep. Tilcara, Maimará, 2 abr. 1943, *Zabala* 564 (paratipo, *A. kloosianus*, CORD, CTES). **La Rioja:** Dep. Capital, La Ramadita, a 25 km de La Rioja, *A. T. Hunziker* 4804 (CORD); a 25 km de La Rioja, 17 feb. 1944, *A. T. Hunziker* 4821 A y B (paratipo, *Amaranthus kloosianus*, CORD; isoparatipo, CTES; isoparatipos, B, MA, S, estos tres no vistos, imágenes!); La Ramadita, a 25 km de La Rioja, 17 feb. 1942, *A. T. Hunziker* 4808 (paratipo, *A. kloosianus*, CORD); La Ramadita, a \pm 25 km de La Rioja, 17 feb. 1944, *A. T. Hunziker* 4810 (paratipo, *A. kloosianus*, CORD); camino a La Esperanza, a \pm 30 km de La Rioja, 7 mar. 1944, *A. T. Hunziker* 5310 (paratipo, *A. kloosianus*, CORD; isoparatipos, MO, F, estos dos no vistos, imágenes!); Ruta Nac. 38 entre La Rioja y Chumbicha, a 15 km de la primera, *F. Biurrum* & *L. Blanco* 7480 (CTES); Dep. Castro Barros, Puerta de Pinchas, 19 feb. 1944, *A. T. Hunziker* 4932 (paratipo, *A. kloosianus*, CORD); Bañados de Pichigasta, feb. 1896, *W. Bodenbender* 8998 (paratipo, *A. kloosianus*, CORD); Dep. Gobernador Gordillo, ca. de la Base Aeronáutica, *Biurrum et al.* 3559 (CTES, SI); Dep.

Famatina, entre Chilecito y Tinogasta, *A. T. Hunziker* 15153 (CORD); Dep. Grl. Ocampo, Ambil, en la ruta 79, entre Tello y Santa Rosa de Catuna, *A. T. Hunziker* 13868 (CORD); ruta 79, 1 km antes de Ambil yendo desde Tello, *A. T. Hunziker et al.* 14039 (CORD); Dep. Grl. San Martín, Ea. El Tala, *D. L. Anderson* 3097 (CORD); campo Balde El Tala, *D. L. Anderson* 3802 (CORD); Dep. Independencia, Patquía, Guayapa, *Lahitte & Castro* 189 (BAB); Dep. Rosario Vera Peñaloza, ruta 20 km 239–242, entre Chepes y El 14, *A. T. Hunziker et al.* 13830 (CORD); Chelcos, *A. T. Hunziker* 14105 (CORD); Ruta Nac. 38, entre Punta de los Llanos y Patquía, *A. T. Hunziker et al.* 15126 (CORD); Dep. Sanagasta, Campo de Huaco, 19 feb. 1944, *A. T. Hunziker* 4938 (paratipo, *A. kloosianus*, CORD); Sanagasta, *A. Soriano* 1008 (SI). **Mendoza:** Dep. La Paz, entre Maquinista Levet y Río Tunuyán, *A. Ruiz Leal* 8992 (LIL); Márgenes del Desaguadero, 12–18 mar. 1944, *J. Semper s.n.* (LIL). **Salta:** Dep. Molinos, entre Seclantás y Brealito, *T. Meyer* 12196 p.p. (LIL); Dep. Rosario de Lerma, Chorrillos, *A. T. Hunziker* 3008, 3010 (paratipos, *A. kloosianus*, CORD); Dep. San Carlos, Amblayo, campo El Durazno, 16 mar. 1943, *A. T. Hunziker* 2630 (paratipo, *A. kloosianus*, CORD, CTES). **San Luis:** Dep. Chacabuco, ca. Concarán, viniendo desde Santa Rosa, *A. T. Hunziker & A. E. Cocucci* 14546 (CORD); Dep. Grl. San Martín, entre Concarán y San Martín, *D. L. Anderson* 2463 (CORD); 2 km al E de San Isidro hacia Concarán, *D. L. Anderson* 2463 (CORD).

II. 24. *Amaranthus lombardoi* Hunz., Bol. Soc. Argent. Bot. 4(1–2): 141. 1951. TIPO: Uruguay. San José: Barrancas del Río Santa Lucía, a orillas del bañado, feb. 1938, *A. Lombardo* 3554 (holotipo, CORD!). Figura 39.

Hierba anual; tallos erectos, delgados, glabros, de hasta 30 cm. Hojas con pecíolo de 0.6–3 cm, glabras, lámina ovado-lanceolada, no ondulada, $2\text{--}5.2 \times 0.9\text{--}2.5$ cm, cuneada en la base, obtusa, acuminada o apenas escotada en el ápice, con margen entero, con breve mucrón. Inflorescencias predominantemente en glomérulos axilares; brácteas y bractéolas ovadas, 1–1.2 mm, más cortas que los sépalos, membranáceas, con la vena media marcada, mucrón 0.1 mm. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con 3 sépalos, terminados en un breve mucrón, 3 estambres. Flores pistiladas con 3 o 4 sépalos naviculares, lineares, algo aquillados, 1.4–1.6 mm, con una leve giba basal, esponjosos y soldados en la base hasta 0.5 mm, con 2 sépalos mayores con 3 o 4 venas, mucronados, y 1 o 2 sépalos menores, lineares, muy angostos, de 0.15–0.2 mm de ancho, con 1 a 3 venas, sin mucrón, todos de igual longitud que los frutos; estigmas 2, brevísimos, 0.10–0.15 mm. Frutos indehiscentes, con pericarpio liso,

Figura 37. *Amaranthus interruptus* R. Br. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A–E, ilustrado de *Jacobs* 1603 (NSW). La barra de escala para A = 1 cm; para B–E = 1 mm.

Figura 38. *Amaranthus kloosianus* Hunz. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A, ilustrado de *Biurrum* 3559 (SI); B–E, de *Lahitte & Castro* 189 (BAB). La barra de escala para A = 1 cm; para B–E = 1 mm.

membranáceo; semillas de color castaño-negruzco, de 1 mm × 0.85 mm, brillantes con algunas punteaduras en el centro y muy punteadas en el margen.

Distribución. *Amaranthus lombardoi* es hasta ahora conocida sólo para Uruguay por su material tipo.

Discusión. *Amaranthus lombardoi* se asemeja a *A. viridis* y a *A. deflexus*. De la primera se distingue porque *A. lombardoi* carece de inflorescencias terminales desarrolladas y cuenta con sépalos engrosados y gibosos basalmente, y frutos de pericarpio liso. Esta característica del pericarpio recuerda a *A. deflexus*, pero esta última especie tiene por lo general sólo dos sépalos y su fruto es netamente mayor que los mismos.

Ejemplares examinados. URUGUAY. **Canelones:** Canelones, Parque Nac. de Carrasco, abr. 1942, *A. Lombardo* 3900 (paratipo, *Amaranthus lombardoi*, CORD).

II. 25. *Amaranthus looseri* Suess., Lilloa 4: 128. 1939. TIPO: Chile. Región Metropolitana de Santiago: Batuco, 25 km al NO de Santiago, 500 m, 7 nov. 1936, *G. Looser* 3620 (lectotipo, designado por Hunziker [1965: 44], GH [ejemplar de arriba] [código de barras] GH00247265!). Figura 40.

Hierba anual; tallos postrados, de hasta 6 cm, débiles, casi glabros, con escasos pelos largos. Hojas con pecíolo de 1.5–7 mm, lámina oblonga, no ondulada, 4–8 × 1.5–3.5 mm, atenuada en la base, obtusa o redondeada en el ápice, sin mucrón, con margen entero, algunas veces algo purpúrea abaxialmente, con la vena media prominente, blanquecina. Inflorescencia en glomérulos axilares; brácteas y bractéolas ovadas a lanceoladas, 0.7–1 mm, más cortas que los sépalos, membranáceas, blanquecinas, ápice agudo, mucrón 0.2 mm. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con 3 o 4 sépalos obovados, 1.25 mm, 3 estambres. Flores pistiladas con (3)4 sépalos espatulados, 1–1.25 mm, redondeados o emarginados, mucronulados en el ápice, más cortos o iguales que el fruto, pero nunca alcanzando los estigmas, membranáceos, blanquecinos en los márgenes, con una vena media amplia, herbácea, de color verde, disímiles entre sí; estigmas

3, cortos, 0.25 mm. Frutos indehiscentes, de pericarpio liso, castaños; semillas de color castaño oscuro, 0.9–1 mm diám, brillantes en el área central, área marginal estrecha y más punteada.

Distribución. *Amaranthus looseri* es una especie endémica de Chile (cerca de Santiago). Florece y fructifica entre noviembre y enero.

Discusión. *Amaranthus looseri* presenta cierta similitud con *A. peruvianus*, aunque se reconocen diferencias evidentes. Las hojas de *A. looseri* tienen ápice entero y carecen de mucrón, las flores estaminadas tienen tres o cuatro sépalos y tres estambres y las pistiladas cuatro (raramente tres) sépalos, mientras que *A. peruvianus* presenta hojas emarginadas y mucronadas, flores estaminadas con uno o dos sépalos y el mismo número de estambres y flores pistiladas con uno (raramente dos) sépalos.

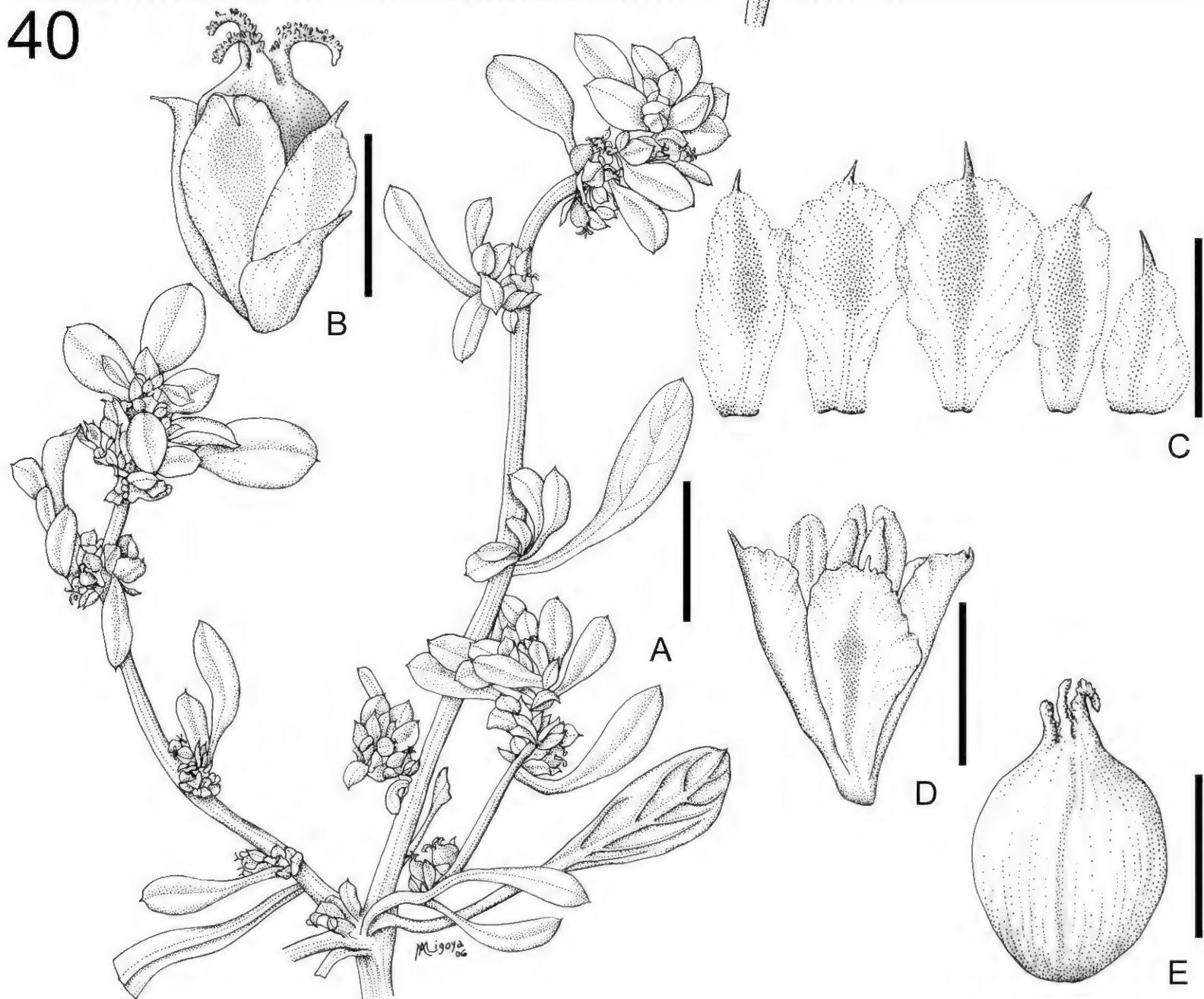
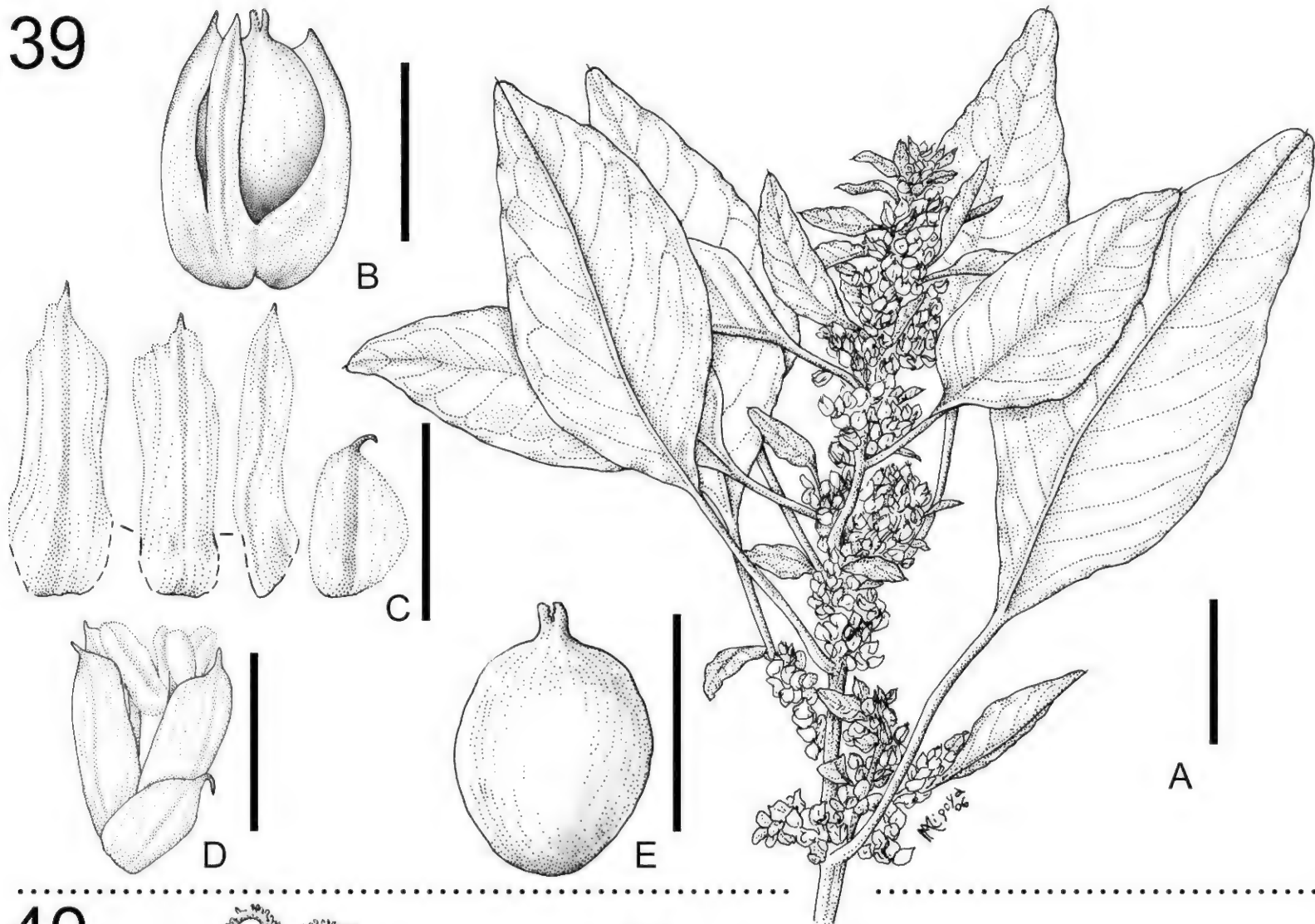
Ejemplares examinados. CHILE. **Región Metropolitana de Santiago:** Santiago, Batuco, 7 nov. 1936, *Looser* 3656 (sintipo, *Amaranthus looseri*, GH); Batuco, ca. de Santiago, ene. 1932, *F. Jaffuel* 1909 (sintipo, *A. looseri*, GH).

II. 26. *Amaranthus macrocarpus* Benth., Fl. Austral. 5: 216. 1870. TIPO: Australia. New South Wales: jct. of Murray & Darling rivers, dic. 1853, *F. Mueller* s.n. (lectotipo, designado por Palmer [2009: 120], MEL-59717 no visto, imagen!; isoelectotipos, MEL-59716 no visto, imagen!, K [código de barras] K000357413 no visto, imagen!). Figura 41.

Hierba anual; tallos erectos o decumbentes, de 15–60 cm, glabros. Hojas con pecíolo de 4–25(–35) mm, lámina ovado-lanceolada, obovada u oblonga, no ondulada, 5–25 × 4–13 mm, atenuada o cuneada en la base, emarginada en el ápice, margen entero, con mucrón. Inflorescencia en glomérulos axilares, oscuros, esféricos, de 6–8 mm diám, formando a veces pseudoespigas foliosas terminales breves de hasta 3 cm; brácteas y bractéolas ovado-lanceoladas, 1(–1.5) mm, agudas en el ápice, mucrón 0.2 mm, membranáceas, con la vena media marcada, más breves que el cáliz. Flores de los dos sexos en la misma inflorescencia. Flores estaminadas con 3(4) sépalos lanceolados a elípticos, 1.1–1.3 mm, agudos u obtusos, membranáceos con la vena media marcada, a menudo terminados en un mucrón de 0.1–0.2 mm,

Figura 39. *Amaranthus lombardoi* Hunz. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A–C, E, ilustrado de *Lombardo* 3254 (CORD); D, de *Lombardo* 3900 (CORD). La barra de escala para A = 1 cm; para B–E = 1 mm.

Figura 40. *Amaranthus looseri* Suessen. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A–E, ilustrado de *Looser* 3620 (GH). La barra de escala para A = 5 mm; para B–E = 1 mm.



3 estambres. Flores pistiladas con 3(5) sépalos angostamente obovados, 1.5–1.8(–3) mm, erectos, agudos, blanquecinos, con la vena media simple o ramificada y de color verde, mucrón o breve arista, 0.3 mm; estigmas 3, engrosados en la base, luego delgados, reflejos, 0.4 mm. Frutos indehiscentes, oblongos o de forma de botella, excediendo en gran medida al cáliz, 2.6–3.2 mm, con el pericarpio inflado, membranáceo, reticulado-rugoso, salvo en el cuarto superior cercano a los estigmas en donde se torna liso, de color verde-amarronado oscuro, más largo que los sépalos; semillas de color castaño-negruzco, $1\text{--}1.25 \times 0.8\text{--}0.9$ mm, muy brillantes en el área central y opacas en el área marginal, pero sin puntuaciones.

CLAVE PARA LA DIFERENCIACIÓN DE LAS SUBESPECIES DE
AMARANTHUS MACROCARPUS

1. Hojas no glaucas; frutos de color verde-castaño oscuro a negro cuando maduros; cáliz con 3(5) sépalos ... *A. macrocarpus* Benth. subsp. *macrocarpus*
- 1'. Hojas glaucas; frutos de color pálido o pajizo cuando maduros; cáliz a veces reducido a sólo 1 o 2 sépalos *A. macrocarpus* Benth. subsp. *pallidus* (Benth.) N. Bayón

II. 26a. *Amaranthus macrocarpus* Benth. subsp. *macrocarpus*.

Amaranthus macrocarpus subsp. *macrocarpus* presenta flores con cáliz generalmente compuesto por 3 (raramente 5) sépalos y frutos de color verde-castaño oscuro a negro cuando maduros.

Distribución y ecología. *Amaranthus macrocarpus* subsp. *macrocarpus* es una subespecie australiana que crece en el centro del distrito de Queensland ca. de Emerald, en el Norte de Victoria, en el Sur y Este del Northern Territory y en el Este de South Australia. Hay dos registros que la consideran maleza: uno en Sydney y el otro en el Centro de Investigación Agrícola de Tamworth. Rara en Gran Bretaña cerca de lugares donde se industrializa lana (distribución tomada de Palmer, 2009). Florece entre los meses de diciembre y abril.

Discusión. *Amaranthus macrocarpus* subsp. *macrocarpus* cuenta con frutos mucho más grandes que el cáliz y por lo tanto se asemeja a *A. deflexus*. Sin

embargo, *A. macrocarpus* tiene tres (raro cinco) sépalos en sus flores pistiladas, mientras que *A. deflexus* tiene dos o tres sépalos. La otra diferencia es que los frutos de *A. deflexus* son lisos mientras que los de *A. macrocarpus* son notablemente rugosos.

Ejemplares examinados. AUSTRALIA. **New South Wales:** 15 km SSE de Wellington, 31 km desde la escuela Dripstone hacia Bussendong Arboretum, *R. Coveny & K. Ingram 10053* (NSW); Central Coast, Saleyards, Flemington, *E. J. McBarron 16155* (NSW); NW slopes, *J. R. Hosking 735* (NSW). **Queensland:** “Armadilla”, *W. Barton 14* (sintipo, *Amaranthus macrocarpus*, MEL-59715 no visto, imagen!); Queensland, Dawson River, *Leichhardt 304* (sintipo, *A. macrocarpus*, MEL-59714 no visto, imagen!).

II. 26b. *Amaranthus macrocarpus* Benth. subsp. *pallidus* (Benth.) N. Bayón, stat. nov. Basónimo: *Amaranthus macrocarpus* Benth. var. *pallidus* Benth., *Flora Austral.* 5: 216. 1870. TIPO: Australia. Queensland: Curriwillighie [Currawillngi], *F. C. Dalton s.n.* (holotipo, MEL-59713 no visto, imagen!; isotipo, K [código de barras] K000357414 no visto, imagen!).

Amaranthus macrocarpus subsp. *pallidus* se caracteriza por sus hojas de tonalidad glauca, con el cáliz reducido a menudo a tan solo 1 o 2 sépalos y frutos de color pálido o pajizo cuando maduros.

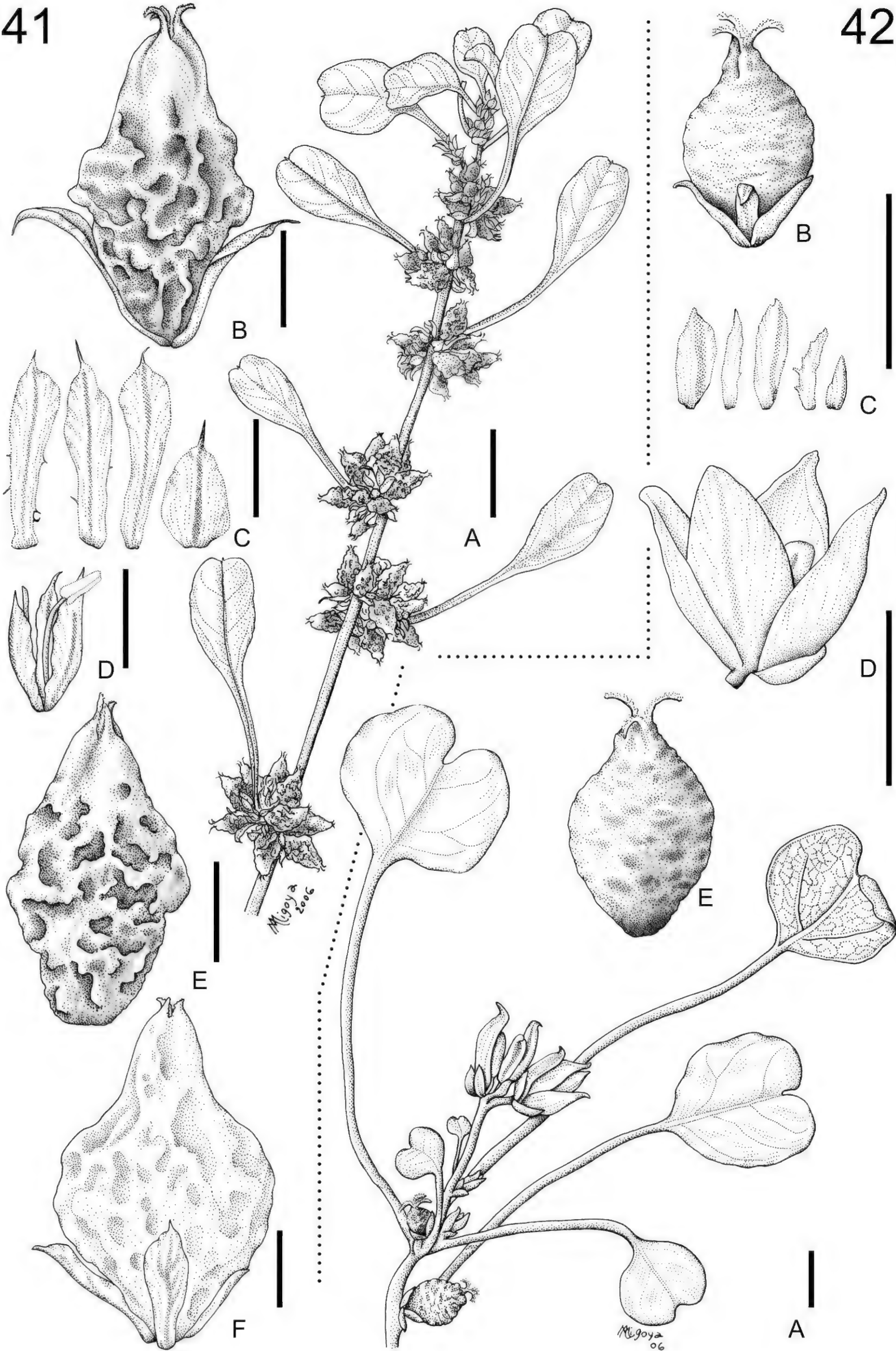
Distribución y ecología. *Amaranthus macrocarpus* subsp. *pallidus* ha sido hallada ca. de Macalister y Noondoo en Queensland, en los alrededores de Brewarrina, Walgett, Garah e Inverell en el norte de New South Wales y en el sudeste de South Australia (distribución tomada de Palmer, 2009). Florece en marzo.

Ejemplares examinados. AUSTRALIA. **New South Wales:** Coocalla, 25 km al O de Garah, *K. L. Wilson 1301* (NSW); 9.7 km al NNO de Inverell sobre la ruta a Grancav, *R. Coveny et al. 12506* (NSW).

II. 27. *Amaranthus minimus* Standl., N. Amer. Fl. 21(2): 119. 1917. *Goerziella minima* (Standl.) Urb., *Repert. Spec. Nov. Regni Veg.* 20: 301. 1924. TIPO: Cuba. Pinar del Río, entre Las Martinas y la costa, *J. A. Shafer 11090* (holotipo, US [código de barras] US00106251!; isotipos,

Figura 41. *Amaranthus macrocarpus* Benth. subsp. *macrocarpus*. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. *Amaranthus macrocarpus* subsp. *pallidus* (Benth.) N. Bayón. —F. Flor pistilada. A–E, ilustrado de *Hosking 735* (NSW); F, de *Wilson 1301* (NSW). La barra de escala para A = 5 mm; para B–F = 1 mm.

Figura 42. *Amaranthus minimus* Standl. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto (NSW). A–E, ilustrado de *Shafer 11090* (US). Las barras de escala para A–E = 1 mm.



NY [cb] NY00073687!, US [cb] US00931033 no visto, imagen!). Figura 42.

Hierba anual; tallos filiformes, postrados, 2–5 cm, ramificados, glabros. Hojas con pecíolo de 3–15 mm, glabras, lámina suborbicular, no ondulada, $1\text{--}3.5 \times 1\text{--}3$ mm, emarginada, ampliamente redondeada en la base, con las venas más oscuras; brácteas y bractéolas ovadas, muy pequeñas, 0.35–0.5 mm, membranáceas, mucho más cortas que los sépalos, vena media apenas evidente. Flores de ambos sexos separadas en la planta, solitarias o en inflorescencias bifloras pequeñas. Flores estaminadas pareadas sobre ramitas pequeñas de 1.5–3.5 mm, con 4 sépalos ovados, 1.2–1.7 mm, membranáceos, con la vena media no ramificada, de color verde, agudos u obtusos, a menudo de ápice recurvado, 4 estambres. Flores pistiladas solitarias o pareadas, casi sésiles, con 4 sépalos lineares, 0.45–0.6 mm, que llegan a la mitad del fruto, membranáceos, agudos, con la vena media inconspicua; estigmas tres(cuatro), 0.2–0.3 mm, delgados. Frutos indehiscentes, 0.9–1.1 mm, lisos o apenas rugosos; semillas de color negruzco, 0.6–0.7 mm diám, punteadas.

Distribución. *Amaranthus minimus* es una especie endémica de la provincia de Pinar del Río, Cuba.

Discusión. *Amaranthus minimus* no se asemeja a ninguna de las restantes especies del género, lo que llevó a Urban (1924) a crear un nuevo género para ella. Tanto Standley (1917) cuando la describe, como Hunziker (1965) no dudan en su pertenencia al género *Amaranthus*. Este último autor es de la idea que esta especie constituiría un subgénero o una sección aparte. Las flores de ambos sexos se hallan en posiciones separadas en una misma planta, cosa que ocurre solamente en *A. spinosus* y en parte en *A. dubius*, pero en lo demás ninguna de estas dos especies poseen semejanza alguna con *A. minimus*.

II. 28. *Amaranthus mitchellii* Benth., Fl. Austral. 5: 214. 1870. *Euxolus mitchellii* (Benth.) F. Muell., Geogr. Cent. Aust.: 214. 1875. *Amaranthus mitchellii* Benth. var. *typicus* Domin, Biblioth. Bot. 89: 78. 1921, nom. inval. TIPO: Australia. Narran River, [probablemente New South Wales], 24 mar. 1846, *T. L. Mitchell* s.n. (lectotipo, designado por Palmer [2009: 121], K [código de barras] K000356723 no visto, imagen!; isoelectotipos, BM [cb] BM000894979 no visto, imagen!, MEL-59723 no visto, imagen!). Figura 43.

Amaranthus mitchellii Benth. var. *strictifolius* Domin, Biblioth. Bot. 89: 78. 1921. TIPO: Australia. Queens-

land: en la base del Mt. Walker, feb. 1910, *K. Domin* s.n. (holotipo, PR-526423 no visto, imagen!).

Hierba anual; tallos principales erectos, ramificados, hasta 40 cm, fuertes y rígidos, glabros. Hojas con pecíolo de hasta 1 cm, glabras, lámina ovado-lanceolada u oblonga, no ondulada, $2\text{--}3.5 \times 0.4\text{--}1.2$ cm, cuneada en la base, obtusa o subaguda en el ápice, con mucrón. Inflorescencias axilares, en glomérulos de 7–8 mm diám, de mayor tamaño en los nudos basales; brácteas y bractéolas ovado-oblongas, 1.8–2.5 mm, más cortas o casi iguales a los sépalos, membranáceas, vena media marcada, de color verde, ápice con una arista erecta o refleja. Flores de ambos sexos sobre una misma inflorescencia. Flores estaminadas con 4 o 5 sépalos ovado-lanceolados, 1.5–2 mm, membranáceos, con la vena media verdosa o parda, marcada, excurrente, 2 o 3 estambres. Flores pistiladas con 5 sépalos espatulados, 2–2.5(–3) mm, adelgazados en una uña en la base, doblados hacia afuera y con márgenes escariosos en la mitad superior, obtusos en el ápice, vena media ramificada, de color verde, subiguales entre sí, mucrón de 0.3 mm; estigmas tres, 0.3–0.5 mm. Frutos indehiscentes, 1.2–1.5 mm (sin incluir a los estilos), con 12 a 15 costillas longitudinales prominentes y onduladas, con un rostro patente de $1 \times 0.7\text{--}1$ mm, formado por las bases infladas de los estilos, iguales en longitud al cáliz; semillas de color castaño-negruzco en el centro y castaño-rojizo en el margen, 1.5×1.3 mm, brillantes en el centro y opacas en el margen.

Distribución y ecología. *Amaranthus mitchellii* es una especie australiana común en la Meseta de Brakly (Northern Territory), distribuyéndose hasta el Lago Eyre al Norte del territorio de South Australia, y hasta el centro de Queensland y el Norte de New South Wales. Existen registros para Western Australia de Roy Hill y Kununurra en las regiones de Pilbara y Kimberley, los que probablemente constituyan introducciones. Encontrada en una oportunidad en Gran Bretaña. Prefiere las planicies de las costas de los ríos y cursos de agua menores, sobre todo luego de la ocurrencia de inundaciones. Ocurre también sobre suelos poco salinos, calcáreos y sobre dunas de arena (distribución y hábitat tomados de Palmer, 2009). Florece entre los meses de (diciembre) abril y julio.

Uso. Hortaliza.

Discusión. *Amaranthus mitchellii* es una especie difícil de confundir con ninguna otra por las prominentes costillas longitudinales y el conspicuo rostro de sus frutos. Sus sépalos son espatulados y

doblados hacia afuera como puede darse en *A. undulatus*, pero en esta última especie se destacan las inflorescencias terminales, careciendo sus frutos de las citadas costillas y siendo además dehiscentes.

Algunos autores (como J. Lindley en Mitchell, 1848) han designado a esta especie con el nombre de *Amaranthus undulatus*, pero no en el sentido dado por R. Brown (1810).

Ejemplares examinados. AUSTRALIA. **New South Wales:** entre el río Darling y Cooper's Creek, *Neilson s.n.* (sintipo, *Amaranthus mitchellii*, MEL-59722 no visto, imagen!; isosintipo, NSW no visto, imagen!); al N en planicies occidentales, 10 km del pantano Yarriarraburra, 29°24'S, 141°5'E, *R. J. Chinnock 3529* (MEL); 35 km NO de Tibboburra, 29°16'S, 141°42'E, dic. 1970, *J. Campbell & J. Pickard s.n.* (NSW). Leichhardt, Peak Downs Mine, 22°55'S, 148°04'E, *G. Burkitt s.n.* (MEL); Sub-Tropical New Holland, 1846, *Mitchell 63* (GH); Charleville, *Giles s.n.* (sintipo, *A. mitchellii*, MEL-59721 no visto, imagen!). **South Australia:** Al NO, entre campo 13 y 14, 27°29'S, 130°25'E, Elder Exploring Expedition, 2 jul. 1891, *R. Helm s.n.* (MEL); Región 2, Lake Eyre South, Gregory Creek, *R. J. Bates 46838* (NSW).

II. 29. *Amaranthus muricatus* (Moq.) Hieron., Pl. Diaph. Fl. Argent.: 227. 1882. Basónimo: *Euxolus muricatus* Moq. in de Candolle, Prodr. 13(2): 276. 1849. TIPO: Argentina. Mendoza: *Gillies s.n.* (lectotipo, designado por Iamónico [2014b: 11], K [código de barras] K000195064 no visto, imagen!; isolectotipo, P [cb] P00609945 no visto, imagen!). Figura 44.

Hierba anual o perenne de corta vida; tallos principales postrados o ascendentes, 25–50 cm, ramificados desde la base, glabros. Hojas con pecíolo de hasta 2 cm, glabras o con escasos pelos en la cara abaxial, lámina linear o linear-lanceolada, algo ondulada, 1.5–8 × 0.2–1 cm, atenuada en la base, redondeada u obtusa en el ápice, a menudo emarginada, con mucrón. Inflorescencias axilares o terminales, las primeras en glomérulos, las segundas en panojas piramidales, a menudo bifurcadas o con más ramas, 2–8 cm, con hojas en la porción basal, verdosas o marrones, frecuentemente con los ejes negruzcos; brácteas y bractéolas deltoides u ovadas, 1–1.5 mm, más cortas que los sépalos pero no menos de la mitad de su longitud, membranáceas, vena media conspicua, ápice agudo, a menudo con un mucrón breve. Flores de ambos sexos sobre una misma inflorescencia. Flores estaminadas con 3 a 5 sépalos obovados, 1.4–2 mm, 3 a 5 estambres. Flores pistiladas con (3)4 o 5 sépalos linear-espatulados, linear-obovados o lanceolados, 1.5–2 mm, con la vena media marcada y en algunos sépalos venas secundarias breves cerca del ápice, obtusos o emarginados, raramente subagudos, iguales entre sí;

estigmas tres, 0.2 mm. Frutos indehiscentes, ± iguales en longitud a los sépalos o apenas excediéndolos, enteramente verrugosos; semillas de color castaño oscuro a negro, 1.2–1.5 mm diám, algo brillantes.

Distribución y ecología. *Amaranthus muricatus* es nativa del Cono Sur de Sudamérica (Argentina, Bolivia [Pedersen, 1999], Paraguay y Uruguay). Introducida en Australia, Europa y Sur de África. Crece entre los 100 y los 1900 m (Pedersen, 1994; Mosyakin & Robertson, 2003). En Argentina y Paraguay florece entre los meses de septiembre y abril, mientras que en España lo hace en mayo.

Nombres vulgares. Ataco, hierba meona, meona, yerba meona (de la Peña & Pensiero, 2004); African amaranth, muricate amaranth (Mosyakin & Robertson, 2003).

Discusión. *Amaranthus muricatus* es una especie semejante a *A. rosengurtii* de la que se diferencia porque esta última tiene sus hojas ovadas, con bractéolas de las flores pistiladas mucho más cortas que los sépalos (la mitad o menores) y sépalos de las flores pistiladas con venas secundarias largas, longitudinales. Por el contrario, *A. muricatus* presenta hojas lineares o angostamente oblongas, bractéolas más cortas que los sépalos, pero a lo sumo llegando a la mitad (no menores) y algunos sépalos de las flores pistiladas con venas secundarias brevísimas en la mitad superior. Las hojas delgadas recuerdan a las de *A. persimilis*, especie que se caracteriza por sus inflorescencias exclusivamente en glomérulos axilares, flores estaminadas con cinco estambres y sépalos de las flores pistiladas espatulados, mientras que *A. muricatus* tiene inflorescencias terminales y axilares, flores estaminadas con tres a cinco estambres y sépalos de las flores pistiladas linear-espatulados, linear-obovados o lanceolados.

Ejemplares examinados. ARGENTINA. **Buenos Aires:** Pdo. Chacabuco, 1922, *C. L. Spegazzini s.n.* (LP); Pdo. Escobar, Ing. Maschwitz, *Lanfranchi 758* (LP); Pdo. Hurlingham, *H. Schwabe 392* (LP); Pdo. La Plata, La Plata, *N. D. Bayón 625b* (LPAG); La Plata, Facultad de Agronomía, 3 ene. 1973, *Panella s.n.* (LPAG); La Plata, Bosque, *A. L. Cabrera 2647, 5201* (ambos en LP); Pdo. San Fernando, Isla Martín García, 6–7 abr. 1928, *A. Castellanos s.n.* (BA); Isla Martín García, *J. Hurrell et al. 3881* (LP). **Catamarca:** Dep. Andalgalá, Andalgalá, *A. T. Hunziker 6847* (CORD); Dep. Belén, Belén, *E. A. Ulibarri 291* (CTES); Dep. Capital, Banda de Varela, *A. Brizuela 1478* (CTES); sin dep. det., Haniyacu, 18 ene. 1930, *A. Castellanos s.n.* (BA). **Chaco:** Dep. 1° de Mayo, Colonia Benítez, *A. G. Schulz 14709* (CTES). **Ciudad Autónoma de Buenos Aires:** Puerto de Buenos Aires, Dársena Norte, *T. M. Pedersen 14552* (CTES). **Córdoba:** Dep. Capital,



Córdoba, La Carolina, ca. del Río Primero, A. T. Hunziker 20249 (CORD); Córdoba, Parque Sarmiento, A. T. Hunziker 6231 (CORD); Barrio Alto Alberdi, L. Ariza Espinar 602 (CORD); Dep. Colón, entre Jesús María y Ascochinga, A. T. Hunziker 6512 (CORD); Dep. Ischilín, Quilino, A. T. Hunziker 6110 (CORD); Deán Funes, A. T. Hunziker 2527 (CORD); Dep. Minas, Sa. de Guasapampa, falda O, ca. de Ojo de Agua, A. T. Hunziker 9167 (CORD); Cordón Occidental, la Bismutina, Castellanos s.n. (BA); Dep. Punilla, Capilla del Monte, A. Castellanos s.n. (BA); Santa María, J. Gutiérrez 238 (CTES); Dep. Río Primero, entre Santa Rosa y Socorro, 5 nov. 1952, A. Castellanos s.n. (CTES); Dep. Río Segundo, Est. Exp. Manfredi 6 (CORD); Dep. San Javier, Sa. Grande, falda O, entre Las Tapias y Las Rosas, A. T. Hunziker 11875 (CORD); Dep. San Justo, 13 km E de La Francia, A. Krapovickas et al. 18518 (CTES); Dep. Santa María, Alta Gracia, A. T. Hunziker 579 (CORD); Dep. Tercero Arriba, Tanacacha, camino a Río Tercero, dic. 1924, A. Scala s.n. (LP); sin dep. det., Mar Chiquita, 21 dic. 1951, Buchinger s.n. (BA). **Corrientes:** Dep. Capital, Corrientes, T. M. Pedersen 1312 (CTES); Dep. Empedrado, Ea. La Yela, T. M. Pedersen 6454 (CTES); Dep. Esquina, entre Tres Bocas y Paso Yunque, A. Krapovickas et al. 27649 (CTES); sin dep. det., s. loc., oct. 1921, C. L. Spegazzini s.n. (LP). **Entre Ríos:** Dep. Gualaguaychú, Ruta 12, Km. 170, A. Burkart et al. 23332 (CTES); A° Gualeyán, A. Burkart et al. 25723 (CTES); Ceibas, A. Burkart 30827 (CTES); Dep. La Paz, Santa Elena, A. Burkart et al. 23329 (CTES); Dep. Nogoyá, Lucas González, Rafaelli 22 (LP). **Formosa:** Dep. Bermejo, Laguna Yema, N. D. Bayón & C. A. Moreno 716, 880 (ambos en LPAG); Dep. Formosa, Guayculec, P. Jörgensen 2565 (LP); Dep. Pirané, Ruta 23, a 5 km de Palo Santo, C. A. Petetin & A. Molina 1033, 1198 (ambos en BAB). **Jujuy:** Dep. Tilcara, Tilcara, A. Krapovickas & C. L. Cristóbal 17564 (CTES); Dep. Tumbaya, entre Purmamarca y Abra Paves, La Ciénaga, A. L. Cabrera et al. 26341 (LP). **La Rioja:** Dep. Chamical, Sa. de los Llanos, frente a Chamical, subiendo a la Qda. de los Godoy, F. Biurrun et al. 7203 (CTES); Dep. Chilecito, Chilecito, Barrio Los Sarmientos, N. D. Bayón 1353, 1355 (ambos en LPAG); Dep. Famatina, Sa. de Famatina, Los Corrales, F. Biurrun et al. 7047 (CTES); Dep. La Capital, Chochangasta, A. T. Hunziker 5140 (CORD); Dep. Grl. Belgrano, Sa. de los Llanos, Dique de Olta, A. T. Hunziker & T. E. Di Fulvio 1443 (CORD); Dep. Sanagasta, A. T. Hunziker 4756 (CORD). **Mendoza:** Dep. Capital, Capital, A. Ruiz Leal 990 (LP); Dep. Maipú, A. Ruiz Leal 2515 (BA); s. loc., 1916, E. Carette s.n. (LP). **Salta:** Dep. Cafayate, Cafayate, 1 ene. 1943, A. Castellanos s.n. (BA). **San Juan:** Dep. Albardón, 5 mar. 1926, A. Castellanos s.n. (BA); Dep. Calingasta, Calingasta, H. A. Fabris & F. O. Zuloaga 8415 (CTES, LP); Dep. Caucete, Caucete, A. Cuezco 1745 (CTES); Dep. Jáchal, Bella Vista, E. R. Guaglianone et al. 2463 (SI); Huerta de Huachi, E. R. Guaglianone et al. 1721 (CTES); Dep. Pocito, a 20 km de San Juan, E. G. Nicora 4306 (SI); Dep. Valle Fértil, San Agustín del Valle Fértil, M. Múlgura et al. 679 (CTES). **San Luis:** Dep. Chacabuco, ca. de Concarán viniendo desde Santa Rosa, A. T. Hunziker & A. E. Cocucci 14553 (CORD); Dep. La

Capital, Dv. Chischaca, 13 dic. 1925, A. Castellanos s.n. (BA); alr. de San Luis, G. Covas 1084 (LP). **Santa Fe:** Dep. Capital, Recreo, A. Ragonese 2056 (BA); Dep. Vera, Dist. Santa Lucía, camino a Fortín Olmos, Tedone 4954 (LP). **Santiago del Estero:** Dep. Aguirre, Ruta Nac. 34, entre Pinto y Casares, A. T. Hunziker & A. E. Cocucci 17815 (CORD); Dep. Choya, Frías, A. T. Hunziker 2522 (CORD); Dep. Rivadavia, Ruta Nac. 34, Selva, A. T. Hunziker & A. E. Cocucci 17767 (CORD); sin dep. det., Cnia. Jaime, 9 nov. 1948, Luna Ruiz s.n. (BAA). **Tucumán:** Dep. Burruyacu, El Timbó, S. Venturi 2438 (BA); Dep. Capital, Villa Luján, S. Venturi 73 (LP); Dep. Trancas, Tapia, S. Venturi 995 (BA); sin dep. det., Río Salí, ene. 1899, s. coll. (LP). **PARAGUAY.** **Boquerón:** Paratodo, P. Arenas 1110 (CTES); Puerto Casado, T. M. Pedersen 4010 (CTES). **Central:** Asunción, oct. 1919, C. L. Spegazzini s.n. (LP). **Presidente Hayes:** Monte Lindo, G. Caballero Marmori 1447 (CTES); Ea. La Perla, T. M. Pedersen 14622 (CTES). **URUGUAY.** **Montevideo:** Montevideo, dic. 1875, Gibert s.n. (LP).

ESPAÑA. **Murcia:** San Javier, 40 km al SE de Murcia, A. Schinini & S. Sánchez García 30576 (CTES); Sucina, 28 km SE de Murcia, A. Schinini & S. Sánchez García 30683 (CTES).

II. 30. *Amaranthus obcordatus* (A. Gray) Standl., N. Amer. Fl. 21: 107. 1917. Basónimo: *Amblogyna urceolata* (Benth.) A. Gray var. *obcordata* A. Gray, Proc. Amer. Acad. Arts 5: 168. 1861. *Amaranthus urceolatus* var. *obcordatus* (A. Gray) Uline & W. L. Bray, Bot. Gaz. 19: 269. 1894. TIPO: Estados Unidos de América. Nuevo México: 1851–52, C. Wright 1746 (holotipo, US [código de barras] US00106265 no visto, imagen!). Figura 45.

Amaranthus urceolatus Benth. var. *jonesii* Uline & W. L. Bray, Bot. Gaz. 19: 269. 1894. *Amaranthus jonesii* (Uline & W. L. Bray) Kov., Nauch. Trud. Vissh Selskostop. Inst. Plovdiv 23(1): 49. 1978. TIPO: Estados Unidos de América. Arizona: Loc. Bowie, 16–21 sep. 1884, M. E. Jones 29 (holotipo, GH [código de barras] GH00037012!; isotipo, US [cb] US00106264 no visto, imagen!).

Hierba anual; tallos principales erectos o ascendentes, ramificados, de hasta 10–50 cm, glabros. Hojas con pecíolo de hasta 8 mm, glabras, lámina oblongo-lanceolada a lanceolado-linear, no ondulada, 1–3 × 0.2–1 cm, atenuada a cuneada en la base, redondeada a truncada en el ápice, con mucrón. Inflorescencias predominantemente axilares, pero formando una aparente espiga hacia el ápice de los tallos, la que carece de hojas o en la que se observan algunas hojas cortas; brácteas y bractéolas ampliamente ovadas, 0.7–1 mm, agudas en el ápice, con la

Figura 43. *Amaranthus mitchellii* Benth. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A–E, ilustrado de Mitchell 63 (GH). La barra de escala para A = 1 cm; para B–E = 1 mm.

Figura 44. *Amaranthus muricatus* (Moq.) Hieron. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A–C, ilustrado de Fabris 8415 (LP); D, E, de Hurrell 3881 (LP). La barra de escala para A = 1 cm; para B–E = 1 mm.

vena media bien marcada, alas membranáceas, más cortas que los sépalos. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con (3–)5 sépalos oblongos, con la vena media marcada, 0.75–1 mm, 3 a 5 estambres. Flores pistiladas con (4)5 sépalos espatulados u obcordados, 1.5–2.25 mm, \pm redondeados y retusos en el ápice, con las vena central y las secundarias marcadas, desiguales, al menos dos de ellos adelgazados en una uña, soldados basalmente; estigmas tres, 0.3–0.5 mm. Frutos indehiscentes, iguales o más cortos que los sépalos, poco rugosos; semillas de color castaño-rojizo, 0.7–0.85 mm diám, muy brillantes y lisas en el área central, más opacas en el área marginal.

Distribución y ecología. *Amaranthus obcordatus* crece en América del Norte, particularmente en los Estados Unidos de América (Arizona, Nuevo México y Texas) y México (Sinaloa y Sonora). Habita en semidesiertos, en ambientes naturalmente disturbados, y crece entre los 1000 m y los 1200 m (Mosyakin & Robertson, 2003).

Nombre vulgar. Trans-pecos amaranth (Mosyakin & Robertson, 2003).

Discusión. *Amaranthus obcordatus* es una especie cercana a *A. torreyi* y *A. fimbriatus*, a las que se asemeja por sus hojas lineares o estrechamente elípticas, sépalos de las flores pistiladas espatulados o flabelados e inflorescencias terminales en espigas no ramificadas. Se distingue de ambas por sus frutos indehiscentes.

II. 31. *Amaranthus pedersenianus* N. Bayón & C. Peláez. Novon 22(2): 133–135, fig. 1. 2012. TIPO: Argentina. Salta: Dep. Cachi, a 46 km de Cachi, camino a Salta, 19 mar. 1972, 3050 m, A. Krapovickas, V. Maruñak, O. Oliva & H. Pueyo 21991 (holotipo, CTES [código de barras] CTES0017272!). Figura 46.

Hierbas probablemente anuales; tallos principales 3–5 ascendentes o erectos, 5–20 cm, glabros. Hojas con pecíolo de 5–12 mm, glabras, lámina angostamente elíptica a elíptica, ondulada, $1.9\text{--}3.3 \times 0.4\text{--}1.4$ cm, atenuada en la base, obtusa o redondeada en el ápice, de color verde oscuro, con mucrón de 0.3–1 mm. Inflorescencias axilares en glomérulos redondeados de

hasta 1 cm diám, de color verde claro con algunos tintes rosados, reunidos en espigas (sin hojas al menos distalmente) 1.5–4 cm; brácteas y bractéolas angostamente ovadas a ovadas, 0.9–2.5 mm, membranosas, con la vena media de color verde, mucrón 0.2–0.5 mm. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con (3)4 o 5 sépalos angostamente elípticos, 2–2.9 mm, obtusos o subagudos, a veces mucronulados, estambres (3)4 o 5. Flores pistiladas con (3)4 o 5 sépalos obovados a espatulados, 2–4 mm, con la lámina de 0.9–2.3 mm de ancho, redondeada a truncada, adelgazados en una uña de 0.2–0.7 mm de ancho, con la vena media ramificada, algo esponjosos en la base, reflejos; estigmas tres, 0.3–0.8 mm. Frutos dehiscentes, con el opérculo rugoso, urna lisa o rugosa, más cortos que los sépalos; semillas de color castaño oscuro a negruzco, $1\text{--}1.5 \times 1\text{--}1.3$ mm, lisas y brillantes en el área central, finamente punteadas y opacas en el área marginal.

Distribución y ecología. *Amaranthus pedersenianus* habita principalmente en las provincias de Salta y Jujuy (Argentina), entre los 2800 m y los 3800 m, a veces en conos de deyección (Hunziker 8073, CORD). Florece entre los meses de enero y marzo.

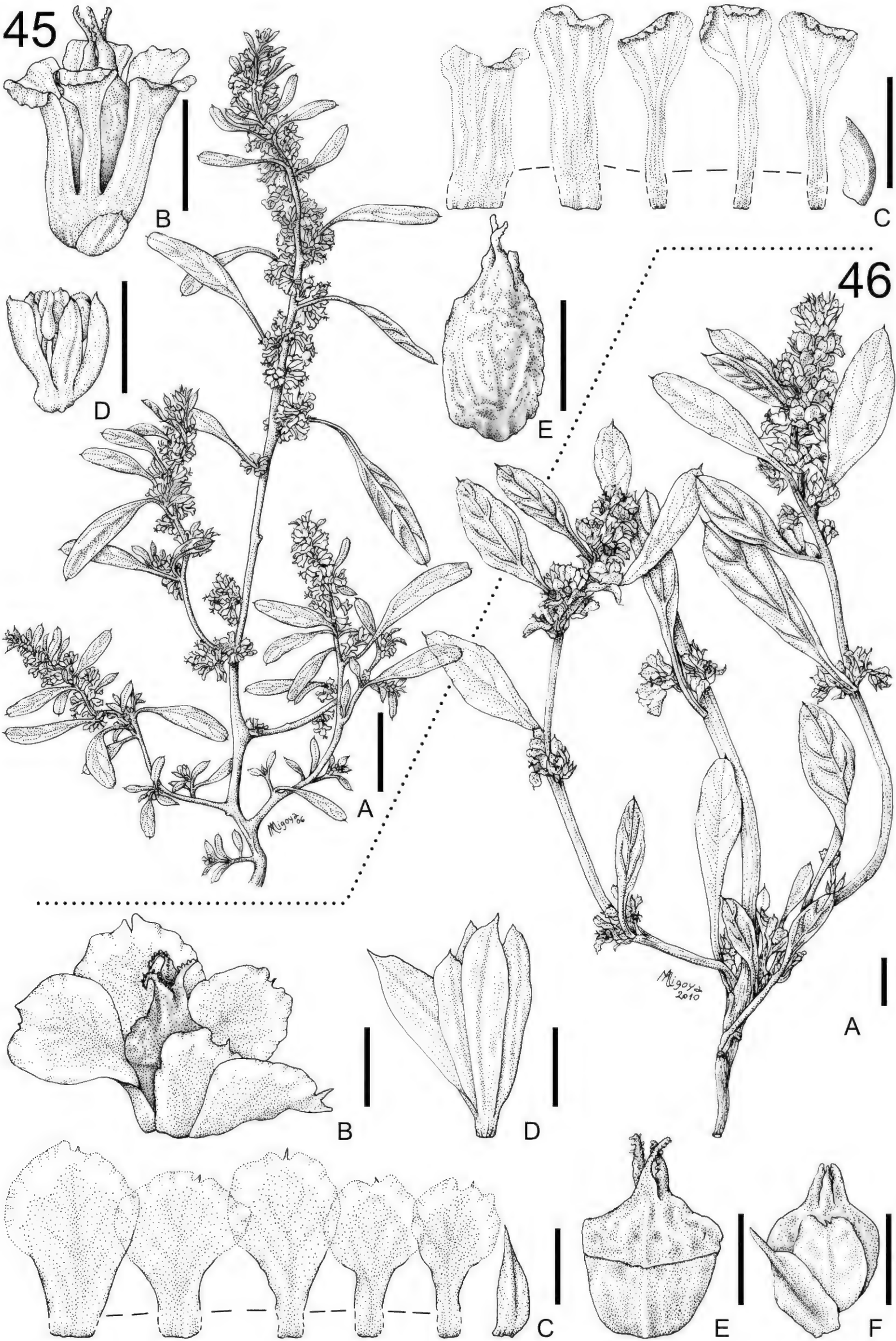
Nombre vulgar. Ataco silvestre (Cabrera 8697, LP).

Discusión. *Amaranthus pedersenianus* es una especie semejante a *A. squamulatus*, *A. kloosianus* y *A. urceolatus* de las que se distingue por sus frutos dehiscentes. Por otro lado, se asemeja a *A. hunzikeri*, pero esta última tiene porte postrado, inflorescencias apicales foliosas y flores estaminadas con tres o cuatro estambres (raramente dos), mientras que *A. pedersenianus* posee porte ascendente o erecto, inflorescencias apicales carentes de hojas y flores estaminadas con tres a cinco estambres. Finalmente, de *A. cardenasianus* se diferencia pues esta especie presenta plantas y hojas más grandes, de 70–100 cm y 4–8 cm respectivamente y siempre cinco estambres, siendo que las plantas de *A. pedersenianus* son menores de 20 cm, sus hojas menores de 4.2 cm y número de estambres variable entre tres y cinco.

Ejemplares examinados. ARGENTINA. **Jujuy:** Dep. Humahuaca, empalme a Iturbe, 20 ene. 1976, A. L. Cabrera et al. 27386 (paratipo, *Amaranthus pedersenianus*, SI).

Figura 45. *Amaranthus obcordatus* (A. Gray) Standl. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A–E, ilustrado de Jones 29 (GH). La barra de escala para A = 1 cm; para B–E = 1 mm.

Figura 46. *Amaranthus pedersenianus* N. Bayón & C. Peláez. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. —F. Flor pistilada con bráctea y un solo sépalo. A–F, ilustrado de A. Krapovickas et al. 21991 (holotipo, CTES). La barra de escala para A = 5 mm; para B–F = 1 mm. Adaptado y rediseñado desde Novon 22(2): 134, fig. 1. 2012.



Salta: Dep. Cachi, entre Payogasta y Tin-Tin, 27 feb. 1965, *J. H. Hunziker 8073* (paratipo, *A. pedersenianus*, CORD); Dep. Rosario de Lerma, Santa Rosa de Tastil, 28 feb. 2005, *G. E. Barboza et al. 1453, 1455 & 1455 bis* (paratipos, *A. pedersenianus*, los tres en CORD); Dep. La Poma, Tipán, Campo de la Paciencia, 12 feb. 1945, *A. L. Cabrera 8697* (paratipo, *A. pedersenianus*, LP); Dep. Los Andes, San Antonio de los Cobres, 7 feb. 1946, *A. L. Cabrera 8971* (paratipo, *A. pedersenianus*, LP).

II. 32. *Amaranthus persimilis* Hunz., Bol. Soc. Argent. Bot. 4(1-2): 133. 1951. TIPO: Argentina. Tucumán: Dep. Tafí, Calimonte, Distr. Amaicha, 1600 m, 22 feb. 1927, *R. Schreiter 5491* (holotipo, CORD!). Figura 47.

Hierba anual; tallos principales erectos, desde pocos cm a 1 m, glabros o glabrescentes, con sólo algunos pelos esparcidos cuando jóvenes. Hojas con pecíolo de 0.2–1.6 cm, glabras, lámina linear a linear-lanceolada, no ondulada, 1–6 × 0.2–0.8 cm, atenuada en la base, aguda o subaguda en el ápice, con mucrón de 0.5 mm. Inflorescencias axilares en glomérulos a veces reunidos en espigas foliosas; brácteas y bractéolas ovado-deltoides, 1.3–1.8 mm, ápice acuminado o mucronado. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con (4)5 sépalos linear-lanceolados a lanceolados, 1.8–2.5 mm, subiguales, agudos o subagudos, mucrón 0.2–0.3 mm, 5 estambres. Flores pistiladas con (4)5 sépalos ampliamente espatulados u obovados, 1.7–3 mm, 1 nervio, mucrón o arista de 0.25–0.4 mm, los externos adelgazados en una uña en la base de 0.1–0.3 mm de ancho, los internos un tanto menores, a veces sin adelgazamiento basal; estigmas 3, de hasta 1 mm. Frutos indehiscentes, más cortos que los sépalos, pericarpio rugoso, con un rostro que soporta los estigmas; semillas de color castaño oscuro, 1.5 × 1.2 mm, brillantes en el área central, más opacas en el margen, que es agudo.

Distribución y ecología. *Amaranthus persimilis* crece en el centro y oeste de la Argentina. Se la encuentra en formaciones leñosas bajas (matorrales), sobre planicies de suelos sueltos y arenosos. Florece entre los meses de enero y mayo.

Discusión. *Amaranthus persimilis* se asemeja por sus hojas lineares a *A. muricatus*, pero se la distingue sin dificultad por su androceo pentámero y por sus sépalos espatulados. En algunos casos, *A. squamu-*

latus podría mostrar similitud por sus hojas, aunque esta última especie tiene flores con al menos algunos de sus sépalos anchos en la base y flores estaminadas con tres estambres. Para Hunziker (1951a) tiene afinidad con *A. cardenasianus*, *A. crispus* y *A. standleyanus*, pero ninguna de estas tres especies tiene hojas lineares o linear-lanceoladas, ni tampoco los sépalos de las flores pistiladas son largamente mucronados. Además *A. cardenasianus* y *A. standleyanus* tienen inflorescencias terminales (no axilares) y *A. crispus* los bordes de las láminas foliares muy ondulados.

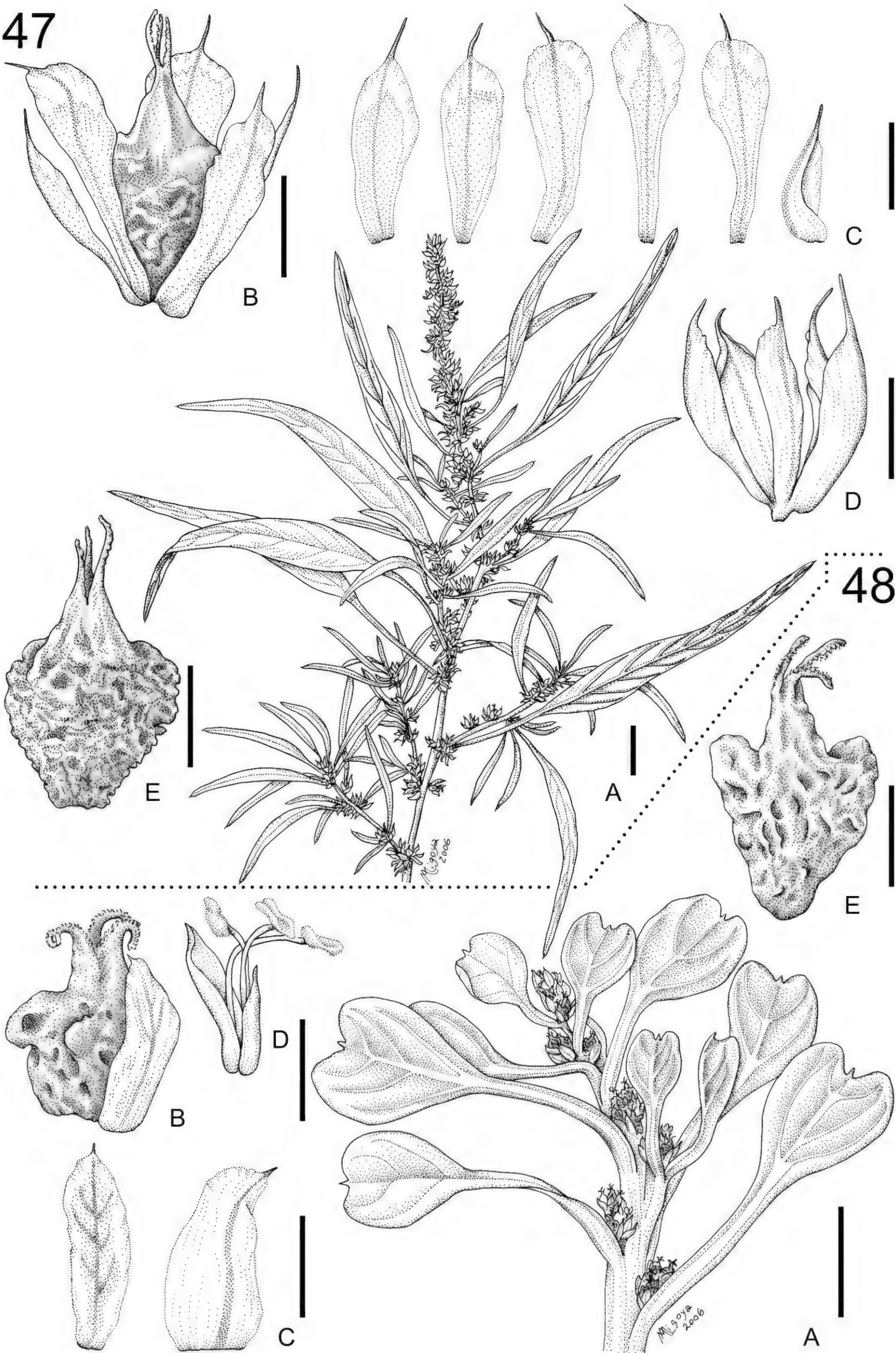
Ejemplares examinados. ARGENTINA. **Catamarca:** Dep. Belén, a 10 km al N de Belén, *A. Lutz & K. Goth 8* (CTES); Dep. Tinogasta, entre Carrizal y Andaluca, *T. M. Pedersen 15314* (CTES); s. loc., *F. Schickendantz 292* (paratipo, *Amaranthus persimilis*, CORD). **Mendoza:** Dep. La Paz, margen derecha del Río Desaguadero, entre los 33°10' y 33°27'S, 5 mar. 1944, *J. Semper s.n.* (CTES); Dep. Santa Rosa, Ruta Nac. 7, Km. 1004, al N de Santa Rosa, *E. G. Nicora et al. 8354* (CTES, SI). **San Juan:** Dep. Caucete, entre las Salinas de Macasín y el río Papagallo, *T. M. Pedersen 15196* (CTES, SI); Pampa de las Salinas, entre los Pj. de Las Liebres y Las Toscas (La Rioja), a 20 km de Las Liebres, *F. Biurrun et al. 4836* (CTES); Dep. Ullún, entre Talacasto y Matagusanó, *R. Palacios et al. 1738* (CTES); s. loc., Km. 810, *C. C. Hosseus 11* (paratipo, *A. persimilis*, CORD).

II. 33. *Amaranthus peruvianus* (Schauer) Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 13(2): 487. 1937. Basónimo: *Mengea peruviana* Schauer, Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur. 19(Suppl. 1): 406. 1843. TIPO: Perú. Puno: Puno, Laguna de Titicaca, alt. 12400', abr. 1833, *F. J. F. Meyen s.n.* (holotipo, B [código de barras] B10-0272701 no visto, imagen!; isotipos, K [cb] K000195016 no visto, imagen!, P [cb] P00609942 no visto, imagen!). Figura 48.

Hierba perenne; tallos principales postrados, de hasta 15 cm, glabros. Hojas con pecíolo de 7(–15) mm, glabras, lámina espatulada a suborbicular, no ondulada, 4–9 × 3.5–6 mm, atenuada en la base, ampliamente redondeada a emarginada en el ápice, con mucrón, con venas y margen blancuzco. Inflorescencia en glomérulos axilares de hasta 15 flores; brácteas y bractéolas ovado-oblongas a elípticas, 0.6–1.4 mm, membranáceas, con la vena media de color verde no ramificada, las alas blanquecinas, acuminadas en el ápice. Flores de

Figura 47. *Amaranthus persimilis* Hunz. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. E. Fruto. A–E, ilustrado de *Pedersen 15196* (SI). La barra de escala para A = 1 cm; para B–E = 1 mm.

Figura 48. *Amaranthus peruvianus* (Schauer) Standl. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalo y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A–C, E, ilustrado de *Cabezas 56* (LP); D, de *Jørgensen 1858* (SI). La barra de escala para A = 5 mm; para B–E = 1 mm.



ambos sexos en la misma inflorescencia. Flores estaminadas con 1 o 2(3) sépalos, 1.5–2 mm, 1 a 3 estambres. Flores pistiladas generalmente con 1, o algunas veces 2 sépalos desiguales, oblongo-elípticos, obovados o espatulados, 0.8–1.5 mm, nervio medio ramificado, borde pestañoso, ápice redondeado, mucronado; estigmas 3, delgados, 0.5–0.6 mm. Frutos indehiscentes, apenas más largos que los sépalos, muy rugosos, a veces con una línea oscura ecuatorial; semillas de color castaño oscuro, 1.2–1.3 × 1 mm, brillantes en el centro y algo más opacas en el margen.

Distribución y ecología. *Amaranthus peruvianus* crece en la Cordillera de los Andes del noroeste de Argentina, Bolivia (Pedersen, 1999) y sur de Perú, en prados húmedos (*Lillo 4117*, CTES) entre los 3500 m y 4500 m. Florece entre los meses de enero y marzo.

Nombre vulgar. Ataco (*Cabezas 56*, LP).

Discusión. *Amaranthus peruvianus* es una especie que comparte con *A. furcatus* el hecho de tener un único sépalo en sus flores pistiladas, aunque en raras excepciones pueden observarse dos. Sin embargo, las hojas son muy distintas, pues en *A. peruvianus* las láminas presentan forma espatulada u orbicular y en *A. furcatus* son lineares o estrechamente obcordadas. Para Hunziker (1965) *A. peruvianus* tiene cierta cercanía con *A. looseri*, pero esta última especie presenta cuatro (raro tres) sépalos en sus flores pistiladas.

Ejemplares examinados. ARGENTINA. **Catamarca:** Dep. Andalgalá, Andalgalá, *P. Jörgensen 1858* (SI); La Ollada, *P. Jörgensen 1858* (LIL-11872); Dep. Santa María, Valle del Cajón, *V. Rodríguez 16780* (CTES). **Jujuy:** Dep. Rinconada, Rinconada Co., cercano al pueblo, *P. Arenas 1901* (CTES). **Tucumán:** Dep. Cerro Muñoz, *M. Lillo 4117* (CTES). PERÚ. **Lima:** Miraflores, Cochinoa, *V. Cabezas 56* (LP).

II. 34. *Amaranthus polygonoides* L., Pl. Jamaic. Pug. 2: 27. 1759. *Roemeria polygonoides* (L.) Moench., *Methodus* (Moench.): 341. 1794. *Amblogyna polygonoides* (L.) Raf., *Fl. Tellur.* 3: 42. 1837. *Albersia polygonoides* (L.) Kunth, *Fl. Berol.* ed. 2, 2: 144. 1838. TIPO: Ilustración en Sloane 1707, vol. 1: 144, tab. 92, fig. 2 (lectotipo, designado por Henrickson [1999: 797], tab. 92, fig. 2 en Sloane, 1707, vol. 1: 144. [El ejemplar de Sloane (Herb. Sloane, 2: 116 [BM-SL no visto, imagen!]) es el que se tomó para efectuar la ilustración, pero no fue visto por Linneo, por lo que no puede ser considerado como material original, de acuerdo a Jarvis et al., 2007: 284]. Figura 49.

Amaranthus berlandieri (Moq.) Uline & W. L. Bray, *Bot. Gaz.* 19: 268. 1894. *Sarratia berlandieri* Moq. in de Candolle, *Prodr.* 13(2): 268. 1849. *Amaranthus polygonoides* L. subsp. *berlandieri* (Moq.) Thell., *Syn. Mitteleur. Fl.* 5(Abth. 1): 352. 1919. TIPO: México. Tamaulipas: entre San Fernando y Matamoros, *Berlandier 2279* (holotipo, G [código de barras] G00236968 no visto, imagen!; isotipos, G [cb] G00236969 no visto, imagen!, G [cb] G00236970 no visto, imagen!, GH [ejemplar de la derecha] [cb] GH00036984 no visto, imagen!, NY [cb] NY00991138 no visto, imagen!).

Hierba anual; tallos principales usualmente prostrados o decumbentes, a veces ascendentes o erectos, 20–50 cm, ramificados, sobre todo en la base, con ramas de 10–40 cm, estramíneos, glabrescentes en la base, pubescentes cerca de la inflorescencia. Hojas con pecíolo de 2–13 mm, lámina ovada u obovado-rómbica, no o apenas ondulada, 3–30 × 2–15 mm, angosta a anchamente cuneada en la base, obtusa o emarginada en el ápice, con mucrón de 0.3–0.7 mm, de color verde grisáceo. Inflorescencias axilares en glomérulos de 0.3–0.7 mm diám, distanciados en la base y próximos en los nudos superiores; brácteas y bractéolas lanceoladas a lineares, 0.8–1.3 mm, de aproximadamente la mitad de longitud que los sépalos, membranáceas, vena media prominente, verdosa, ápice acuminado. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con (4)5 sépalos lanceolados, desiguales, 0.7–1.3 mm, agudos o subagudos, 2 estambres. Flores pistiladas con el cáliz de aspecto tubular, con 5 sépalos espatulados, 1.7–2.5 mm, inflados y coalescentes en un tramo basal de 0.6–0.9 mm (aproximadamente 1/3 del largo de la flor), en la mitad superior doblados hacia afuera, expandidos, obtusos en el ápice, algunas veces con una pequeña muesca u otras veces agudos, no siempre con mucrón de 0.2 mm; membranáceos, 3-nervados, vena media no ramificada, de color verde; sépalos engrosados basalmente, permitiendo ver el ovario en la porción media; tubo del cáliz 0.7–1 mm diám, porción expandida distal 1.4–2 mm diám, más larga que el fruto; estigmas 3, engrosados en la base, de aprox. 0.5–0.7 mm. Frutos indehiscentes o tardíamente dehiscentes, con la parte superior rugosa, base cilíndrica, envuelta por el tubo del cáliz y soldada al mismo; semillas de color castaño-rojizo a negro, 0.8–1 × 0.7 mm, brillantes.

Distribución y ecología. *Amaranthus polygonoides* se distribuye por toda la región del Caribe y Centroamérica, Estados Unidos de América (Texas) y México. Esta especie prefiere ambientes disturbados, áreas costeras, costado de caminos, o sedimentos de arcilla (*Schinnners 30872*, CORD), hasta los 500 m de altitud (Mosyakin & Robertson, 2003). Esta especie

ha sido introducida en Europa y Asia. Florece en noviembre.

Nombres vulgares. Smartweed amaranth, tropical amaranth (Mosyakin & Robertson, 2003).

Discusión. Es correcto lo expresado por Henrickson (1999) cuando sostiene que *Amaranthus polygonoides* carece de rasgos que permitan distinguirla de *A. berlandieri*. En efecto, en ambas taxa las flores se reúnen en glomérulos axilares, con pedúnculos no engrosados a la madurez, con los sépalos de las flores pistiladas unidos basalmente en una zona esponjosa y con tres nervaduras y con frutos indehiscentes o dehiscentes. Por otra parte, es semejante a otras especies de flores urceoladas como *A. anderssonii*, *A. kloosianus*, *A. squamulatus* y *A. urceolatus*. *Amaranthus anderssonii* es la más cercana, pero *A. polygonoides* se distingue de ella por sus plantas más ramosas y sus semillas más grandes (Eliasson, 1985). Además sus hojas son ovadas, no espatuladas como en *A. anderssonii*. De las otras tres especies se diferencia por el androceo, siendo que en *A. polygonoides* es dímero, pentámero en *A. kloosianus* y trímero en *A. squamulatus* y *A. urceolatus*.

En la Flora de China (Bojian et al., 2003) se incluye a la especie *Amaranthus taishanensis* F. Z. Li & C. K. Ni, caracterizada por poseer cinco sépalos en sus flores pistiladas, dos (o tres) estambres en las estaminadas y frutos indehiscentes. En dicho tratamiento florístico aparece una nota de los autores remarcando la posibilidad de que este taxón constituya una sinonimia de *A. polygonoides*. Los autores también encuentran una semejanza con *A. blitum*, aunque reconocen que el número de sépalos de las flores pistiladas no coincide entre ambas especies. El tipo (F. Z. Li 116) fue solicitado a los herbarios de PE y SDFS pero no se pudo confirmar la existencia de este ejemplar.

En la descripción original, Linneo (1759) menciona “*Sloane. Jam. l. t. 92. f. 2*” (Sloane, 1707: 144) donde el taxón fue designado por el polinomio “*Blitum polygonoides viride, seu ex viridi et albo variegatum, polyanthos*”. Henrickson (1999) explica que Linneo sólo vio la figura de Sloane y no el ejemplar sobre el que se basó el dibujo, de ahí que dicho espécimen (Herb. Sloane 2: 116, BM) no puede ser designado como lectotipo (se han observado las imágenes digitales de ambos). Henrickson (1999) designa al dibujo que aparece en Sloane (1707) como tipo. La lámina original 92 de Sloane y el ejemplar de Sloane, del cual fue dibujado, están depositados en BM. Sloane (1707: 144) expresa: “It grows in hard Clay grounds, and amongst Rubbish, every where about the Town of St.

Fago de la Vega”. Kellogg (1988) trata al ejemplar de Sloane como tipo, pero por las razones expuestas por Henrickson no correspondería considerarlo como lectotipo.

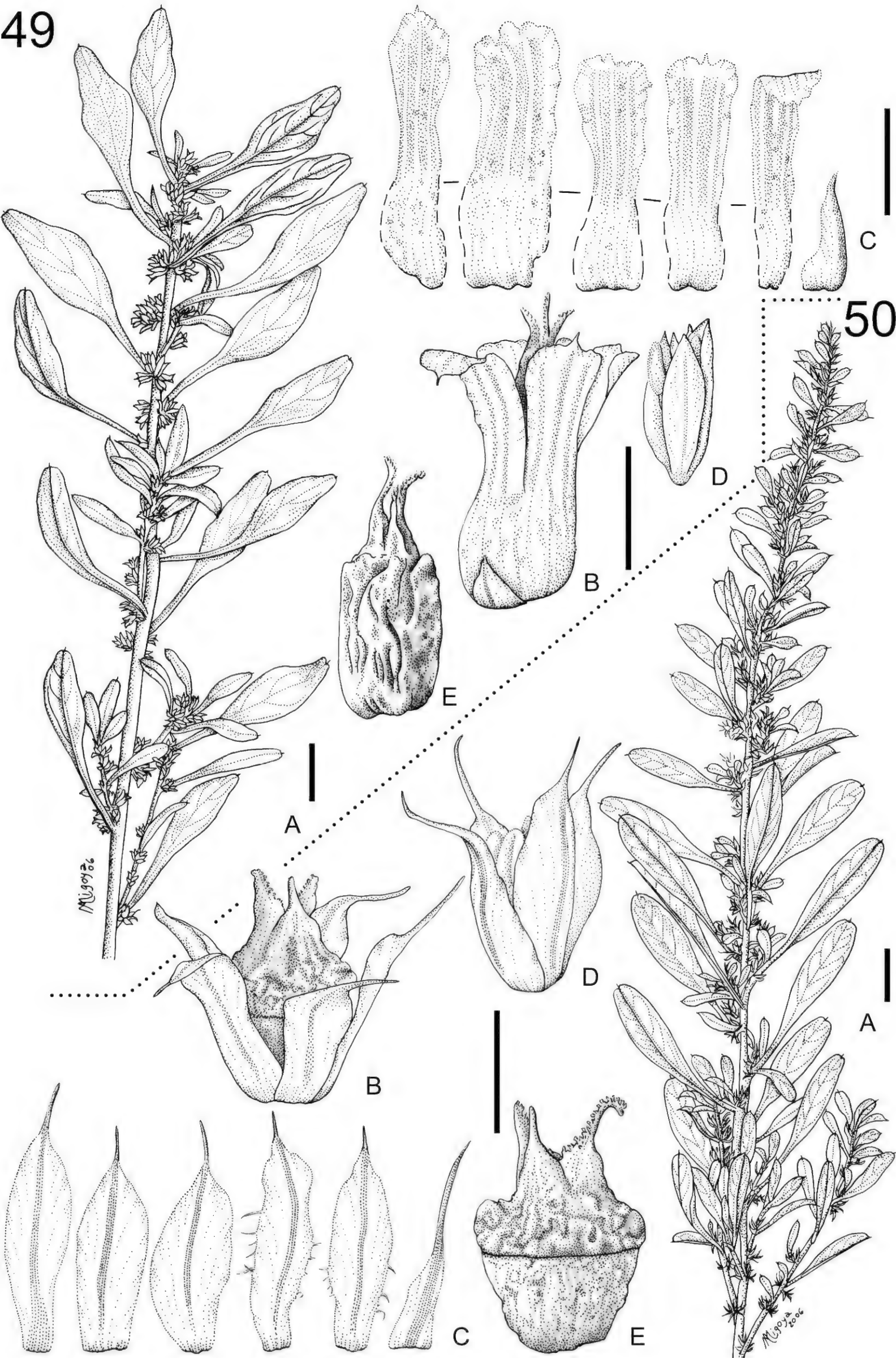
Ejemplares examinados. ESTADOS UNIDOS DE AMÉRICA. **Texas:** Ca. Temple, Bell Co., S. E. Wolff 40 (US); Brownsville, R. Runyon 5936 (CTES, LIL), 5943 (BA, CTES); S Texas, R. Runyon 2350 (US); Willacy Co., 2 mi. al O de Raymondville, L. H. Shinnars 30872 (CORD); Maverick Co., 4.7 mi. al N de Eagle Pass, L. H. Shinnars 30842 (CORD); Presidio Co., 10 mi. NW de Shafter, arriba de Cibolo Creek, ca. de Cieniguita, L. C. Hinckley & B. H. Warnock 46827 (LIL). GUATEMALA. Lago Petén Itzá, R. Tún Ortiz 1219 (US).

MÉXICO. **Tamaulipas:** ca. Victoria, E. Palmer 543 (US). **Yucatán:** Yucatán, Yuhamkamb, F. Gaumer 1778 (CTES).

II. 35. *Amaranthus praetermissus* Brenan, J. S. African Bot. 47(3): 478. 1981. TIPO: Sudáfrica. North Transvaal: Malalahoek 20 km al NE de Messina, 7 feb. 1976, J. P. M. Brenan 14143 (holotipo, K [código de barras] K000195015 no visto, imagen!; isotipos, NBG [cb] NBG0127903-0 no visto, imagen!, PRE [cb] PRE0637853-0 no visto, imagen!). Figura 50.

Hierba anual; tallos principales erectos, 0.20–1 m, ramificados principalmente en la base, glabros, papilosos cuando jóvenes. Hojas con pecíolo de 10–15 mm, glabras, lámina oblonga a casi linear, no ondulada, 1–4 × 0.1–1 cm, atenuada en el base, obtusa a subaguda en el ápice, mucronada. Inflorescencias en glomérulos axilares de 0.4–0.6 mm diám, que tienden a confluir hacia el ápice de los tallos, debido a que los entrenudos se hacen más breves, originando en apariencia una inflorescencia terminal foliosa; brácteas y bractéolas lanceoladas, 0.75–2.2 mm, más cortas que los sépalos, espinescentes. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con 4 sépalos ovados, 2 mm, mucronados, 3 o 4 estambres. Flores pistiladas, con 4 o 5 sépalos lanceolados a oblongo-lanceolados, 1.5–3 mm, con acumen erecto o divergente, 0.25–1 mm, (raramente redondeados), vena media no ramificada de color verde; estigmas tres, 0.5–0.75 mm. Frutos dehiscentes, con el opérculo rugoso, más cortos que el cáliz; semillas de color castaño-negruzco, 1–1.2 × 0.75–1 mm, brillantes.

Distribución y ecología. *Amaranthus praetermissus* crece en África austral desde Angola (Brenan, 1981), Botswana, Namibia y Zimbabwe hacia el sur. A veces considerada como maleza de cultivos (Brenan 14172, K) y de jardines (Brenan, 1981). Florece entre los meses de diciembre y marzo.



Discusión. *Amaranthus praetermissus* es muy semejante a *A. clementii* (Australia), *A. blitoides* (América del Norte) y *A. persimilis* (América del Sur). Estas cuatro especies se parecen por sus hojas delgadas, sus inflorescencias en glomérulos axilares y sus frutos dehiscentes (salvo en *A. persimilis*). *Amaranthus clementii* tiene los sépalos de las flores pistiladas obtusos a emarginados, mientras que las otras dos especies los tienen agudos. *Amaranthus blitoides* tiene hojas más anchas que *A. praetermissus*, generalmente mayores de 5 mm de ancho, sépalos de las flores pistiladas desiguales entre sí, con un mucrón de 0.2 mm, mientras que *A. praetermissus* tiene hojas menores de 5 mm de ancho, con los sépalos casi iguales entre sí, con un acumen conspicuo de 0.25–1 mm. De *A. persimilis* se la puede distinguir porque esta última tiene sépalos espatulados y frutos indehiscentes, mientras que *A. praetermissus* los tiene lanceolados o lanceolado-oblongos y sus frutos son dehiscentes.

Según Brenan (1981) sería cercana a *Amaranthus schinzianus*, pero esta última especie tiene los sépalos de las flores pistiladas espatulados u obovados, mientras que *A. praetermissus* los tiene lanceolados u oblongo-lanceolados.

Ejemplares examinados. BOTSWANA. **Ghanzi y Kgalelagadi:** *C. Skarpe S-411* (K). NAMIBIA. Haikamchab, *E. E. Galpin & H. Pearson 7529* (SAM). SUDÁFRICA. **North Cape:** Kimberley, 88 mi. al O de Douglas, *R. H. Compton 23999* (NBG). **North Transvaal:** Messina, *J. P. M. Brenan 14172* (K). **South West Africa:** Sandfontain, *M. Wilman s.n.* (SAM). ZIMBAWE. **Matabeleland South:** Gwanda, *A. J. Norris-Roger 664* (K).

II. 36. *Amaranthus pumilus* Raf., Med. Repos., ser. 2, 5: 360. 1808. TIPO: Estados Unidos de América. New Jersey, Mant[ua], s.f., *Rafinesque-Schmaltz s.n.* (lectotipo, designado por Macklin et al. [2005: 275], PH [código de barras] PH00002353 no visto, imagen!). Figura 51.

Hierba anual; tallos principales postrados a ascendentes, 0.10–0.40 m, ramificados, glabros, carnosos, a menudo con tonalidades de color rojizo. Hojas agrupadas en los extremos de los tallos, con pecíolo de 5–10 mm, lámina suborbicular, ampliamente ovada u obovada, ondulada, 0.6–1.5 × 0.8–1.5 cm, glabra, carnosa, atenuada o cuneada en la base, redondeada a obtusa en el ápice, mucronada.

Inflorescencias axilares en glomérulos verdosos; brácteas y bractéolas ovadas a elípticas, 1.2–2 mm, alcanzando a la mitad de los sépalos, membranáceas. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con 5 sépalos angostamente oblongos, 5 estambres. Flores pistiladas con 5 sépalos oblongo-obovados a lineares, 2–4 mm, obtusos, subiguales; estigmas tres, 0.3 mm. Frutos indehiscentes, más largos que los sépalos, lisos o apenas rugosos, o con costillas verticales; semillas de color castaño oscuro, 2.5 × 1.5 mm, lisas en el centro y punteadas en el margen.

Distribución y ecología. *Amaranthus pumilus* crece en un área restringida de dunas de la costa oriental de Estados Unidos de América e islas del Atlántico. Es una especie que se considera amenazada (Mosyakin & Robertson, 2003). Se la encontrado en flor entre los meses de febrero y agosto.

Nombres vulgares. Seabeach amaranth, coast amaranth (Mosyakin & Robertson, 2003; Macklin et al., 2005).

Discusión. *Amaranthus pumilus* es una especie difícil de confundir con ninguna otra debido a que sus tallos y hojas son carnosos, tendiendo estas últimas a agruparse en el extremo de los vástagos.

Ejemplares examinados. ESTADOS UNIDOS DE AMÉRICA. Black Island, *S. T. Olney s.n.* (K). **New Jersey:** Atlantic City, 12 ago. 1866, *C. F. Parker s.n.* (K). **South Carolina:** Onslow Co., *S. W. Leonard 5002* (SI).

II. 37. *Amaranthus rhombeus* R. Br., Prodr. Fl. Nov. Holland: 414. 1810. *Euxolus rhombeus* (R. Br.) Moq. in de Candolle, Prodr. 13(2): 275. 1849. TIPO: Australia. Áreas tropicales de Northern Territory y Queensland: “North Coast”, mayo 1802, *R. Brown* [Iter Australiense] 3050 (holotipo, BM [código de barras] BM000522509 no visto, imagen!; isotipo, K [cb] K000356722 no visto, imagen!).

Hierba de hasta 22 cm. Hojas con pecíolo de 1–2.5 cm, lámina elíptica, ovado-elíptica o rómbica, 2–3 × 0.9–1.8 cm, atenuadas en la base, obtusas o redondeadas, algo emarginadas en el ápice; brácteas

←
Figura 49. *Amaranthus polygonoides* L. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A, ilustrado de Wolff 40 (US); B–E, de Tún Ortíz 1219 (US). La barra de escala para A = 1 cm; para B–E = 1 mm.

Figura 50. *Amaranthus praetermissus* Brenan. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A–E, ilustrado de Brenan 14172 (K). La barra de escala para A = 1 cm; para B–E = 1 mm.

y bractéolas de hasta 2 mm, más cortas o igualando a los sépalos, agudas y mucronadas. Inflorescencias principalmente en pseudoespigas terminales, de 4–6 × 0.3 cm, sin hojas, delgadas, aunque pueden observarse glomérulos axilares de 3 mm diám. Flores estaminadas con 3 sépalos, 3 estambres. Flores pistiladas con 3 sépalos, mayores que el fruto. Fruto dehiscente, globoso, rugoso.

Distribución. *Amaranthus rhombeus* es una especie poco frecuente de Australia, hallada principalmente a lo largo de la costa norte, en Northern Territory, en las penínsulas de Cobourg y Gove. También se la ha coleccionado en el NE de Queensland en las cercanías de Chillagoe y Mungana (distribución tomada de Palmer, 2009).

II. 38. *Amaranthus rosengurtii* Hunz., Kurtziana 3: 201. 1966. TIPO: Uruguay. Flores: Arroyo Grande, Ea. Santa Adelaida, 21 nov. 1937, *B. Rosengurt, Gallinal, Aragone, Bergalli & Campbell PE-1031* (holotipo, CORD!). Figura 52.

Hierba perenne; tallos principales decumbentes o ascendentes, 15–40 cm, glabros. Hojas con pecíolo de 2–5 mm, glabras, lámina ovada o angostamente ovada, raramente elíptica, no ondulada, (0.9–)1.8–2.7 × 0.3–1 cm, usualmente atenuada o algunas veces cuneada en la base, usualmente redondeada o emarginada en el ápice, con mucrón de 0.3 mm. Inflorescencias terminales en cortas panojas apicales; brácteas y bractéolas oblongas, 1–1.4 mm, de la mitad o menos en longitud con respecto a los sépalos, membranáceas, vena media de color verde. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con 4 o 5 sépalos oblongos, 3 o 4 estambres. Flores pistiladas con (4)5 sépalos oblongos o lanceolados, 2–3.8 mm, agudos u obtusos en el ápice, con la vena media conspicua y con algunas venas secundarias largas, sépalos iguales, más o menos superpuestos en los bordes; estigmas tres, 0.1–0.2 mm. Frutos indehiscentes, apenas rugosos en la base, a veces notablemente rugosos en la parte superior cerca de los estigmas, más cortos que los sépalos; semillas de color negro, 1.2–1.5 mm, poco brillantes.

Distribución y ecología. *Amaranthus rosengurtii* crece en el centro, S y NO de Uruguay y centro–este de la Argentina (Entre Ríos). Esta especie ha sido

colectada desde el sur de Brasil (Rio Grande do Sul). Encontrada en campos y en vías férreas (*Rosengurt 7213*, CORD). Florece entre los meses de diciembre y abril.

Discusión. *Amaranthus rosengurtii* es una especie muy cercana a *A. muricatus*, aunque esta última presenta hojas lineares o angostamente oblongas, mayores de 4 cm de longitud, (en *A. rosengurtii* son ovadas y menores de 2.5 cm), bractéolas algo menores que los sépalos de las flores pistiladas, superando la mitad de su longitud (en *A. rosengurtii* son a lo sumo de la mitad de la longitud de los sépalos) y algunos sépalos de las flores pistiladas poseen venas secundarias brevísimas, sólo visibles en la mitad superior (en *A. rosengurtii* las venas secundarias son varias y largas).

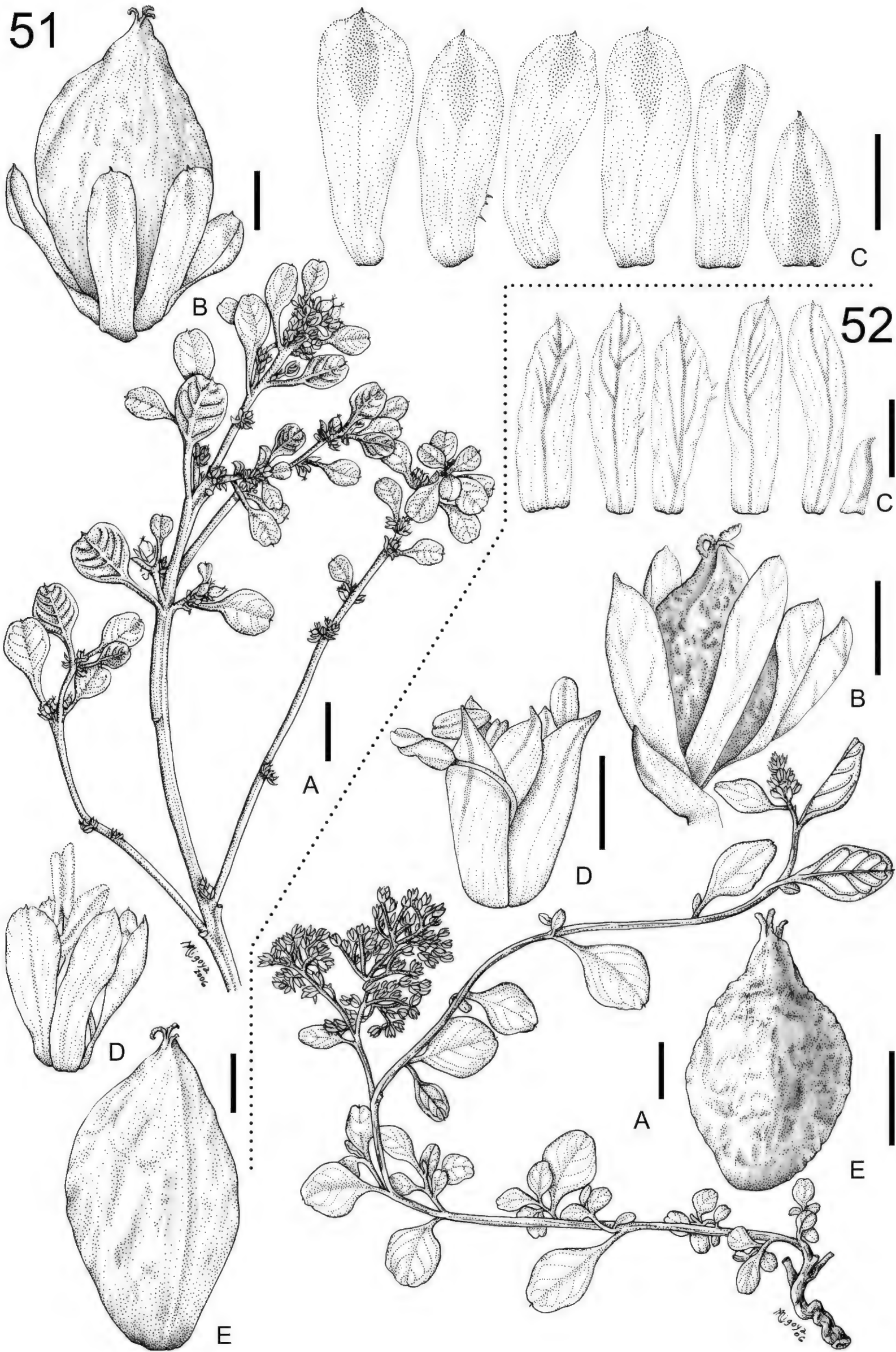
Ejemplares examinados. ARGENTINA. **Entre Ríos:** Dep. Gualaguaychú, Gualaguaychú, *A. Burkart et al.* 25727 (CTES, SI); Dep. La Paz, 42 km al SE de La Paz, ca. de El Yeso, *A. Burkart* 25925 (CTES, SI); Dep. Nogoyá, Crucecitas, Ea. Las Aguadas, 26 feb. 1964, *T. M. Pedersen s.n.* (CTES-379542). BRASIL. **Rio Grande do Sul:** al O de Alegrete, *A. Capivarí, M. M. Arbo & A. Schinini* 2424 (CTES). URUGUAY. **Artigas:** Bella Unión, 7 feb. 1958, *B. Rosengurt B-7213* (paratipo, *Amaranthus rosengurtii*, CORD); Catalán, Ruta 30, 4 dic. 1957, *B. Rosengurt B-6844* (paratipo, *A. rosengurtii*, CORD). **Florida:** San Pedro del Timote, 14 dic. 1936, *B. Rosengurt et al. PE-198* (paratipo, *A. rosengurtii*, CORD). **Lavalleja:** Ruta 8, Km. 189, camino a Minas, *V. Solís Neffa et al.* 286 (CTES). **Salto:** Carumbé, *T. M. Pedersen* 16203 (CTES); A. Bayucúa y Río Daymán, *B. Rosengurt et al.* 10324 (CTES).

II. 39. *Amaranthus schinzianus* Thell. in Schinz & Thellung, Vierteljahrsschr. Naturf. Ges. Zürich 57: 535–537. 1912. TIPO: Deutsch Süd west Afrika [Namibia], Gross Namaland, abr. 1889, *Fleck 171a* (lectotipo, aquí designado, Z [código de barras] Z000000247!; isolectotipo, M [cb] M0107380 no visto, imagen!). Figura 53.

Hierba anual; tallos principales postrados a erectos, 10–30 cm, más o menos ramificados, especialmente abajo pero a veces en toda la planta, glabros. Hojas con pecíolo de 3–15 mm, glabras, lámina linear a oblongo-lanceolada, no o apenas ondulada, 5–32 × 1–7 mm, atenuada en la base, obtusa en el ápice, mucronada. Inflorescencias axilares, en glomérulos densos a lo largo de los

Figura 51. *Amaranthus pumilus* Raf. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A–E, ilustrado de *Leonard 5002* (SI). La barra de escala para A = 1 cm; para B–E = 1 mm.

Figura 52. *Amaranthus rosengurtii* Hunz. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A–C, ilustrado de *Burkart 25925* (SI); D, E, de *Rosengurt B-6844* (CORD). La barra de escala para A = 1 cm; para B–E = 1 mm.



tallos, que confluyen hacia el ápice de los mismos dando una inflorescencia foliosa; brácteas y bractéolas lanceoladas u ovadas, 0.60–0.75 mm, más cortas que los sépalos, agudas. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con 4 o 5 sépalos elípticos a oblongos, subagudos u obtusos, blanquecinos, 4 o 5 estambres, anteras 0.6–0.7 mm. Flores pistiladas con 4 o 5 sépalos espatulados a obovados, 0.8–1.7 mm, blanquecinos con la vena media de color verde, no ramificada, redondeados u obtusos en el ápice, algunas veces provistos de un corto mucrón; estigmas tres, 0.25–0.3 mm. Frutos indehiscentes o dehiscentes, fuertemente verrugosos, sobre todo en su mitad superior, de color castaño a la madurez, más largos que los sépalos; semillas de color castaño-negruzco, ± 1 mm diám, brillantes en el área central, algo opacas en el área marginal.

Distribución y ecología. *Amaranthus schinzianus* es endémica del sur y suroeste de África (Namibia, Sudáfrica). Esta especie prefiere planicies de arenas rojas cubiertas de pastos duros y con algunos arbustos esparcidos, a la sombra de los cuales suele cobijarse (Davidse & Loxton 6166, US). *Amaranthus schinzianus* fue introducida en el Reino Unido de Gran Bretaña como parte de impurezas de la lana (Brenan, 1981). Florece entre los meses de enero y junio.

Discusión. *Amaranthus schinzianus* es una especie semejante a *A. praetermissus*, presentando la primera sépalos de las flores pistiladas de forma espatulada u obovada, truncados o mucronados en el ápice, mientras que la segunda muestra sépalos de las flores pistiladas lanceolados u oblongo-lanceolados con un acumen de 0.25–1 mm.

En la descripción original Thellung (in Schinz & Thellung, 1912: 536) menciona dos sintipos: *A. Rehmann 2983* y *Fleck 171a*, los que se hallan depositados en el herbario Z. Se han estudiado ambos ejemplares y se designa al segundo como lectotipo de *Amaranthus schinzianus* por presentar una planta más completa cuyos caracteres se corresponden con los del protólogo.

Ejemplares examinados. NAMIBIA. Nakop Railway Station, Shale, *W. Marais 1112* (K); 8 km on Great

Karasberg rd. from the Karasburg/Grunau rd., *Oliver & Steenkamp 6264* (K); **Great Namakwaland:** Klein Karas, Groendoorn, in lapios, *I. Örtendahl 367* (K). SUDÁFRICA. **North Cape:** 31 km al O de Kakamas a lo largo de la ruta a Pofadder, *G. Davidse & A. Loxton 6166* (US). **West Cape:** Beaufort West Div., Nelspoort, *S. G. Lewis 4243* (SAM); Bitterfontein (Bosjesmanslop), *K. L. P. Zeyher 1438* (SAM); Kapkolonie: Kaup, Flakkvaal, *A. Rehmann 2983* (sintipo, *Amaranthus schinzianus*, Z [código de barras] Z000000248).

II. 40. *Amaranthus sclerantoides* (Andersson) Andersson, Kongl. Svenska Vetensk. Acad. Handl., 1859: 59. 1861. Basónimo: *Euxolus sclerantoides* Andersson, Kongl. Svenska Vetensk. Acad. Handl., 1853: 163. 1853 [1855]. TIPO: Ecuador. Galápagos: Isla Charles [Santa María], “Hab. locis cultis pinguioribus in insula Charles (Galapagos), Maj. 1852”, *N. J. Andersson s.n.* (lectotipo, aquí designado, S-07-12532 no visto, imagen!; isotipos, GH [código de barras] GH00037038!, S-R-256 no visto, imagen!). Figura 54.

Amaranthus sclerantoides f. *hoodensis* B. L. Rob. & Greenm., Amer. J. Sci., ser. 3, 50: 140. 1895. TIPO: Ecuador. Galápagos: Isla Hood [Española], jul. 1891, *G. Baur 288* [Dr. George Baur se observó como el colector del material Galápagos por Robinson & Greenman, 1895: 135] (holotipo, GH [código de barras] GH00135646 no visto, imagen!; isotipo, GH [cb] GH00135647 no visto, imagen!).

Amaranthus sclerantoides f. *chathamensis* B. L. Rob. & Greenm., Amer. J. Sci., ser. 3, 50: 140. 1895. TIPO: Ecuador. Galápagos: Isla Chatham [San Cristóbal], SW end, lower region, Wreck Bay, jul. 1891, *G. Baur 289* (holotipo, GH [código de barras] GH00135644 no visto, imagen!; isotipo, GH [cb] GH00135645 no visto, imagen!).

Amaranthus sclerantoides f. *abingdonensis* A. Stewart, Proc. Calif. Acad. Sci., ser. 4, 1: 54. 1911. TIPO: Ecuador. Galápagos: Isla Abingdon [Pinta]: “occasional among rocks at 700 ft.”, *A. Stewart 1359* (holotipo, CAS-86542 no visto, imagen!).

Amaranthus sclerantoides f. *albemarlensis* A. Stewart, Proc. Calif. Acad. Sci., ser. 4, 1: 55. 1911. TIPO: Ecuador. Galápagos: Isla Albemarle [Isabela], Turtle Cove, 25 abr. 1905–1906, *A. Stewart 1360* (holotipo, CAS-86543 no visto, imagen!; isotipo, SI!).

Amaranthus sclerantoides f. *rugulosus* J. T. Howell, Proc. Calif. Acad. Sci. 21: 94. 1933. TIPO: Ecuador. Galápagos: Isla Indefatigable [Santa Cruz o Chávez], Academy Bay, *J. T. Howell 9062* (holotipo, CAS-203292 no visto, imagen!; isotipo, K!).

Figura 53. *Amaranthus schinzianus* Thell. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A, ilustrado de *Rehmann 2983* (Z); B–E, de *Davidse & Loxton 6166* (US). La barra de escala para A = 1 cm; para B–E = 1 mm.

Figura 54. *Amaranthus sclerantoides* (Andersson) Andersson. —A. Hábito fértil. —B. Hoja. —C. Hoja. —D. Flor pistilada. —E. Sépalos y bráctea de la flor pistilada. —F. Flor estaminada. —G. Fruto. —H. Fruto. A, D–G, ilustrado de *Andersson s.n.* (GH); B, de *Stewart 1359* (CAS); C, de *Stewart 1360* (SI); H, de *Howell 9062* (K). Las barras de escala para A–C = 1 cm; para D–H = 1 mm.



Hierba anual; tallos postrados o ascendentes, 5–40 cm, teretes, glabros, de color verde claro. Hojas con pecíolo poco diferenciado de 2–12 mm, glabras, de forma variable: desde linear y apenas dilatada en el ápice o linear-obcordada, hasta obcordada o cuneada, ampliamente dilatada apicalmente, no ondulada, $3\text{--}25 \times 1\text{--}5$ mm, muy gradualmente atenuada en la base, por lo que se hace difícil reconocer el punto donde se inicia el pecíolo, truncada, obtusa o emarginada, con mucrón de 0.4 mm. Inflorescencias en glomérulos axilares, más densos hacia el ápice; brácteas y bractéolas linear-lanceoladas, 1.25–2 mm, más cortas que los sépalos, ápice agudo. Flores de ambos sexos sobre una misma inflorescencia. Flores estaminadas sostenidas por un pedúnculo corto y grueso de 0.15–0.3 mm long, con (2)3 sépalos linear-lanceolados, 1.4–2 mm, (2)3 estambres. Flores pistiladas con 3 o 4 sépalos linear-lanceolados, 1.6–2.25 mm, igual o apenas más largos que el ovario maduro, algunas veces igualando a los estigmas, agudos en el ápice, a veces corchosos y engrosados en la base, al menos 1 o 2 sépalos con la vena media ramificada, desiguales; estigmas tres, 0.5 mm. Frutos dehiscentes o indehiscentes, pero en el último caso con una línea ecuatorial más oscura, lisos a rugosos; semillas de color negro, $0.95\text{--}1.1 \times 0.8\text{--}1$ mm, brillantes, con el margen agudo.

Distribución y ecología. *Amaranthus sclerantoides* es un endemismo de las Islas Galápagos, que prefiere los terrenos bajos cercanos a las costas, explanadas más elevadas formadas por materiales calcáreos o planicies arenosas y de suelos rojos un poco más alejadas de la costa (Svenson 20, K). Esta especie se encuentra rara vez en el interior de las islas. Florece entre los meses de enero y abril.

Discusión. *Amaranthus sclerantoides* tiene cierta afinidad con *A. furcatus* pues sus hojas son lineares y el margen de sus semillas es marcadamente agudo. Sin embargo, *A. sclerantoides* presenta flores estaminadas con tres (raramente dos) sépalos y tres (raramente dos) estambres y flores pistiladas con tres o cuatro sépalos. Por su parte, *A. furcatus* tiene un sépalo en ambos tipos de flores y un solo estambre.

Andersson (1853 [1855]: 163) describe *Euxolus sclerantoides* y en el protólogo menciona “Hab. Locis siccis regiones inferiores insulae Charles (Ipse).” En el herbario S existen dos especímenes que se corresponden con la diagnosis original, que llevan los números S-07-12532 y S-R-256, mientras que en GH existe un tercer ejemplar. Se selecciona al ejemplar S-07-12532 pues presenta numerosos tallos en floración cuyos caracteres responden a lo

expresado en el protólogo y en cuya etiqueta se especifica la fecha de colección.

En un principio se pensó en la existencia de formas que se circunscribían en su distribución a las distintas islas del archipiélago de las Galápagos y en función de ello tanto Robinson y Greenman (1895) como Stewart (1911) y Howell (1933) les dieron sus nombres distintivos. Luego se comprobó que esto no era así y que distintos tipos conviven sobre las mismas islas y en las mismas poblaciones. Por esta razón, se sigue el criterio de Wiggins y Porter (1971) al no brindar categoría de forma a las variantes morfológicas observadas dentro de *Amaranthus sclerantoides*.

Ejemplares examinados. ECUADOR. **Galápagos:** Isla Santa Cruz, Pelican Bay, *P. S. Bentley* 150 (K); Isla Santa Cruz, Bahía Academy, *H. K. Svenson* 20 (K); Isla Santa Cruz, a lo largo de la “ruta nueva” que va desde Bahía Academy a Bella Vista, *I. L. Wiggins* 18433 (LIL); Isla Santa María, Post Office Bay, *J. T. Howell* 8809 (LIL).

II. 41. *Amaranthus scleropoides* Uline & W. L. Bray, Bot. Gaz. 19: 316. 1894. *Amaranthus blitoides* S. Watson var. *scleropoides* (Uline & W. L. Bray) Thell., Syn. Mitteleur. Fl. 5(Abth. 1): 293. 1919. TIPO: Estados Unidos de América. Texas: “Western Texas to El Paso”, 2 ago. 1849, *C. Wright* 582 p.p. (lectotipo, designado por Henrickson [1999: 790], GH [código de barras] GH00037010!; isoelectotipo, US [cb] US00106262 no visto, imagen!). Figura 55.

Hierba anual; tallos principales ascendentes o decumbentes en los nudos inferiores, volviéndose luego erectos, 15–60 cm, glabros. Hojas con pecíolo de 2–25(–40) mm, glabras, lámina lanceolada o angostamente rómbica, no ondulada, (10–)15–30(–40) \times 2–10 mm, glauca, atenuada hacia la base, reondeada o retusa en el ápice, mucronada; brácteas y bractéolas ovado-trianguulares, ± 1.5 mm, más cortas que los sépalos, herbáceas, aquilladas, ápice acuminado o mucronado, mucrón 0.25 mm. Inflorescencias axilares en glomérulos, con sus ejes engrosados e inflados, endurecidos a la madurez. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con (4)5 sépalos oblongos a lanceolado-acuminados, (1.2–)1.5–2.2 mm, membranáceos, con la vena media muy marcada, 3 estambres. Flores pistiladas con 5 sépalos espatulados u oblongo-espatulados, 1.2–2.5 mm, uninervios, aquillados, erectos o reflejos, con una mancha de color verde en el centro, uña basal endurecida, engrosados y unidos en la base, similares en longitud, pero el interno más delgado; estigmas 2 o 3, con la base de los mismos inflada y esponjosa,

0.4–0.7 mm. Frutos dehiscentes, con el opérculo tuberculado a liso, urna lisa, más cortos que los sépalos; semillas de color castaño oscuro a negro, 0.9–1.1 mm, brillantes.

Distribución y ecología. *Amaranthus scleropoides* es una especie que crece en los Estados Unidos de América (Texas) y México (Tamaulipas) (Mosyakin & Robertson, 2003). Esta especie prefiere áreas abiertas y secas, aunque también se la puede encontrar en ambientes disturbados y sobre sedimentos calcáreos grisáceo-castaños (*Shinners 30814*, CORD), crece entre el nivel del mar y los 1300 m (Mosyakin & Robertson, 2003). Se la ha encontrado en floración entre los meses de abril y julio, y entre octubre y diciembre.

Nombres vulgares. Bonebract amaranth, bonebract pigweed (Mosyakin & Robertson, 2003).

Discusión. *Amaranthus scleropoides* es una especie próxima a *A. crassipes*, aunque vegetativamente *A. scleropoides* es de hábito más erecto, dando como resultado plantas más altas. Sus frutos son dehiscentes, de pericarpio algo tuberculado a liso y con 2–3 ramas estigmáticas. Por su lado, las plantas de *A. crassipes* son hierbas de hábito decumbente, sus frutos son indehiscentes, de pericarpio conspicuamente tuberculado en la mitad superior y con 2 (raramente 3) ramas estigmáticas.

Ejemplares examinados. ESTADOS UNIDOS DE AMÉRICA. **Texas:** Texas Agricultural Exp. Station, Edwards Co., *V. L. Cory 44562* (CORD); Kinney Co., 6 mi. E de Brackettville, *L. H. Shinners 30814* (CORD); Travis Co., *B. C. Tharp & F. Barkley 15591* (CORD); SW Texas, Corpus Christi Bay, *E. Palmer 1130* (GH); A. A. Heller 1894 (US); Austin, *R. H. Painter 384* (US); Cameron Co., S Texas, 2 mi. S de San Benito, *R. Runyon 2169* (US).

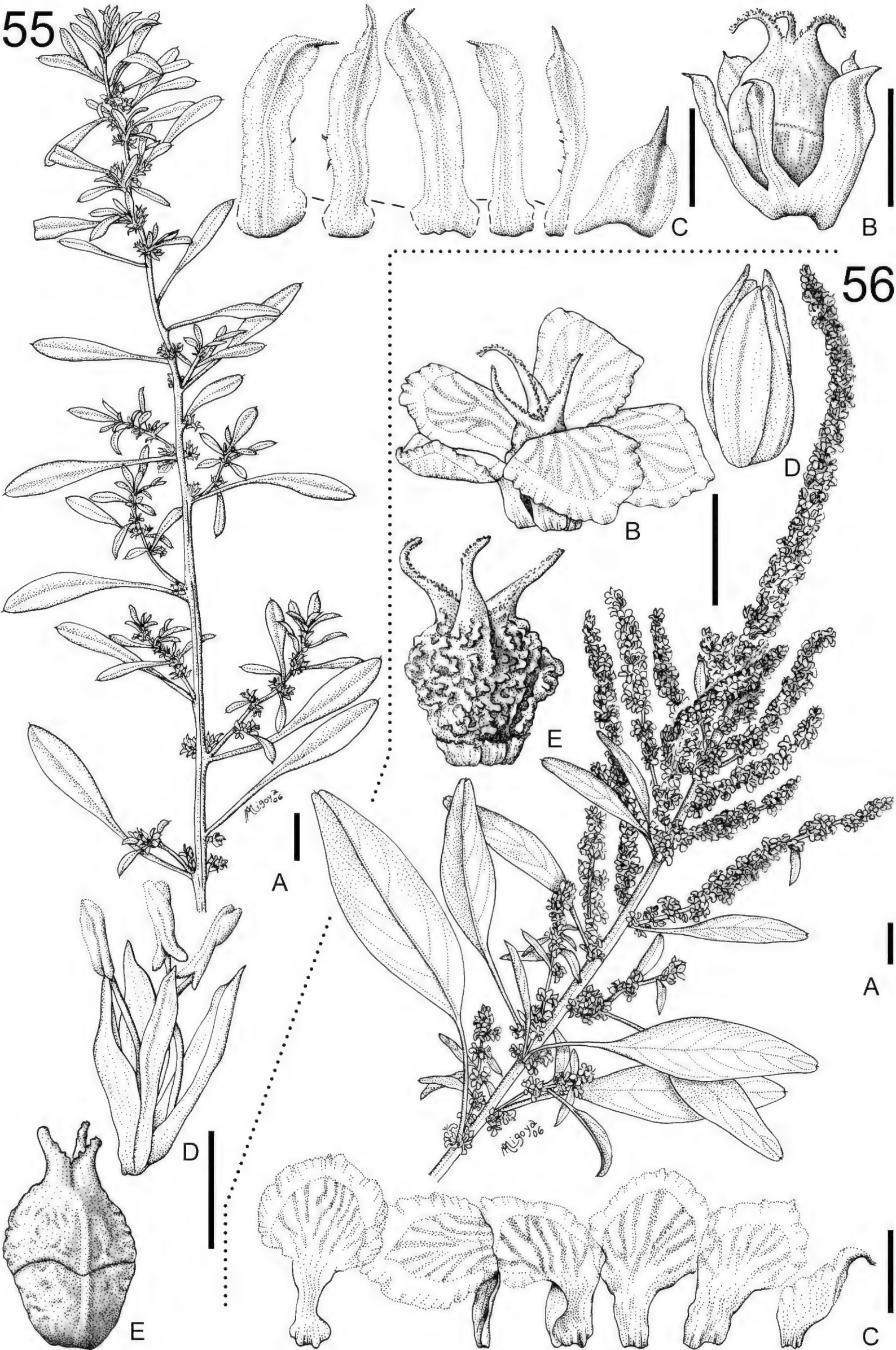
II. 42. *Amaranthus squamulatus* (Andersson) B. L. Rob., Proc. Amer. Acad. Arts. 43(2): 22. 1907. Basónimo: *Scleropus squamulatus* Andersson, Kongl. Svenska Vetensk. Akad. Handl., 1853 [1855], ser. 3, tab. 41: 162. 1855. TIPO: [Ecuador.] Galápagos: Chatam [sic, Chatham; Isla San Cristóbal], 1853, *N. J. Andersson s.n.* (lectotipo, aquí designado, S-06-2324 no visto, imagen!). Figura 56.

Amblogyna squarrolusa A. Gray, Proc. Amer. Acad. Arts 5: 169. 1861, como “*Amblogyne*”. *Scleropus squarrolusus* Andersson in A. Gray, Proc. Amer. Acad. Arts 5: 169. 1861, pro syn. *Amaranthus squarrolusus* (Andersson) Uline & W. L. Bray, Bot. Gaz. 19: 270. 1894, TIPO: [Ecuador.] Galápagos, s.d., *N. J. Andersson 69* (lectotipo, aquí designado, K [código de barras] K000582940 no visto, imagen!)

Hierba anual; tallos principales erectos, más raramente decumbentes con ramas erectas, 0.2–1 m, simples o ramificados, subglabros a glabros, o pubescentes cerca de las inflorescencias. Hojas con pecíolo 0.4–2 cm, glabras, lámina de forma variable, lanceolada, oblonga, ovada o angostamente elíptica, no ondulada, $2-6 \times 0.3-2$ cm, muy gradualmente atenuada en la base, subaguda a redondeada en el ápice, con mucrón de 1 mm. Inflorescencias axilares y terminales, las primeras en glomérulos redondeados, 0.5–1 cm diám o en breves espigas, las terminales espiciformes, $5-20 \times 0.5-1.5$ cm, simples o con pocas ramas, conformadas por la confluencia de glomérulos axilares próximos con hojas que se hacen más breves hacia el extremo apical; brácteas y bractéolas ovadas a ovado-lanceoladas, 1.5–3.5 mm, por lo general más cortas que los sépalos aunque algunas veces pueden superarlos, espinescentes, vena media de color verde, acuminadas con una arista erecta, endurecidas en la base, envolviendo apretadamente los ejes de la inflorescencia. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con 5 sépalos lanceolados, 1–2 mm, 3 estambres. Flores pistiladas con 5 sépalos espatulados, 2–3 mm, expandidos y doblados hacia fuera, redondeados a agudos y acuminado-aristados en el ápice, usualmente desiguales, el interno más pequeño; sépalos con vena media simple o ramificada, con un escudo central verdoso y endurecido, escariosos en el margen, inflados y connados en la base, flores más anchas que largas, con el cáliz expandido en flores plenamente desarrolladas de 3.5–5 mm diám en la porción distal; estigmas 3, engrosados en la base, divergentes, 1 mm. Frutos usualmente indehiscentes, con el pericarpio liso o rugoso, fuertemente envueltos por los sépalos; semillas de color negro, 1.15×1 mm, brillantes, puntuadas en el área central.

Distribución y ecología. *Amaranthus squamulatus* crece en Ecuador continental (Guayas) y en las Islas Galápagos (Eliasson, 1987). Prefiere las planicies de sabanas, ambientes con vegetación leñosa achaparrada y márgenes de lagunas temporarias. También fue hallada sobre suelos arenosos (*Holm-Nielsen et al. 2065*, AAU), en playas y en lugares rocosos costeros hasta los 30 m de altitud. Florece entre los meses de marzo y junio.

Discusión. *Amaranthus squamulatus* es muy similar a *A. urceolatus*, diferenciándose por sus flores más grandes, con tubo más breve y más ancho, bases de los sépalos menos engrosadas en el fruto y una tendencia a que sus brácteas sean más gruesas con la



edad y tiendan a envolver los ejes de la inflorescencia.

Andersson (1853 [1855]: 162) al describir *Scleropus squamulatus* menciona en el protólogo: “Hab. locis graminosis regionis inferioris isulae Chatham (Ipse).” En el herbario S existen dos especímenes que se corresponden con la diagnosis original: *Andersson s.n.* (S06-2324) y *Andersson 115* (S-R-257). Entre ambos, se selecciona como lectotipo al ejemplar *Andersson s.n.* (S06-2324) pues sus caracteres se ajustan a lo expresado en el protólogo, presenta mayor abundancia de inflorescencias y en su etiqueta se especifica la fecha y la localidad de colección.

Amblogyna squarrulosa fue descrita por A. Gray (1861: 169) basándose en la morfología de las flores pistiladas, sin citar material tipo, y escribiendo luego del nombre lo siguiente: “(*Scleropus squarrulosus*, Anderss. ined., from the Galapagos)”. Es muy probable que Gray haya tenido en sus manos el ejemplar *Andersson 69* depositado en K [código de barras] K000582940, en cuyo ángulo inferior derecho posee una etiqueta en la que se lee: “69, *Scleropus squamulatus*, Galapagos”. Aparentemente, Gray comete un error al transcribir el epíteto específico y usa *squarrulosus* en lugar de *squamulatus*, el empleado por Andersson. Se designa al ejemplar *Andersson 69* como lectotipo dado que, como se dijo anteriormente, Gray no mencionó material tipo y dicho ejemplar ha sido el único localizado, y tal vez, el único estudiado por Gray al describir su especie.

Ejemplares examinados. ECUADOR. **Galápagos:** Chatham [Isla San Cristóbal], *N. J. Andersson 115* (sintipo, *Scleropus squamulatus*, S-R-257); Isla Santa Cruz, Conway Bay, *J. T. Howell 9863* (US); Isla Santiago, *W. Morton Wheeler et al. 44* (US); Isla Isabela, Tagus Cave, *A. Stewart 1362* (US). **Guayas:** 400 m al E de Punta Carnera, *L. B. Holm-Nielsen et al. 2065* (AAU); entre Ancón y Atahualpa, *L. B. Holm-Nielsen et al. 2097* (AAU); 1 km al NO de Chanduy hacia Atahualpa, *L. B. Holm-Nielsen et al. 2128* (AAU, MO); Punta de Santa Elena, *L. B. Holm-Nielsen et al. 2323* (AAU, MO); 3 km S de Pacoa, ca. 27 km N de Santa Elena, *L. B. Holm-Nielsen et al. 2442* (AAU, MO).

II. 43. *Amaranthus standleyanus* Parodi ex Covas, Darwiniana 5: 339. 1941, nom. reemplazo. Sin. reemplazado: *Amaranthus parodii* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 17(3): 240. 1937, non *A. parodii* Thell., Repert. Spec. Nov.

Regni Veg. 24: 301. 1927, nomen; et in Physis, 9: 8, descr. 1928. TIPO: Argentina. Tucumán: Amaicha, 2300 m, 2 feb. 1933, *L. R. Parodi 11040* (holotipo, F-685296 no visto, imagen!). Figura 57.

Amaranthus vulgatissimus Thell., Syn. Mitteleur. Fl. 5 (Abth. 1): 343. 1919, non *Amaranthus vulgatissimus* Speg., Anal. Mus. Nac. Buenos Aires 7: 135. 1902. TIPO: Argentina. Salta: Metán, dic. 1905, *C. L. Spegazzini 167* (holotipo, Z [código de barras] Z000000249!).

Hierba anual; tallos principales erectos o decumbentes, de 30–50 cm, ramificados, glabros en la base, con algunos pelos ensortijados hacia el ápice. Hojas con pecíolo de 1.8–5 cm, glabras o apenas pubescentes a lo largo de las venas en la cara inferior cuando jóvenes, lámina lanceolada, ovada o redondeado-rómbica, no o algo ondulada, 1.5–4 × 0.4–2.4 cm, atenuada o cuneada en la base, gradualmente adelgazada hacia el ápice, frecuentemente obtusa, emarginada, a veces aguda, con mucrón de 0.5–0.8 mm. Inflorescencias principalmente axilares, en glomérulos de 0.5–1 cm diám, o terminales, en panojas densas a espiciformes, foliosas o no de 5–10 × 1(–1.5) cm; brácteas y bractéolas ovadas a ovado-lanceoladas, 0.5–2 mm, más cortas que los sépalos, membranáceas, ápice agudo, con mucrón 0.25–0.4 mm. Flores de ambos sexos en una misma inflorescencia. Flores estaminadas con 5 sépalos oblongo-lanceolados, 1.25–2.75 mm, agudos, mucronados, 5 estambres. Flores pistiladas con 5 sépalos espatulados, 1.5–2.8 mm, cada uno 0.5–1 mm de ancho en la parte distal, adelgazados en una uña basal de 0.1–0.3 mm de ancho, redondeados en el ápice, mucrón 0.5 mm, reflejos, con la vena media pocas veces ramificada; estigmas 3, de 0.5–1 mm. Frutos indehiscentes, algunas veces con un rostro, arrugados, más o menos del largo de los sépalos; semillas de color castaño-rojizo a negro, 1.2–1.5 × 1 mm, brillantes.

Distribución y ecología. *Amaranthus standleyanus* es una especie característica del centro y noroeste de Argentina y del Paraguay. Naturalizada en Europa. Esta especie prefiere planicies de suelos arenosos, a la sombra de arbustos y subarbustos, acequias y lechos rocosos de cursos secos (*Cantino 727*, CORD), banquinas de caminos y terraplenes de

Figura 55. *Amaranthus scleropoides* Uline & W. L. Bray. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A, B, ilustrado de *Heller 1894* (US); C–E, de *Runyon 2169* (US). La barra de escala para A = 1 cm; para B–E = 1 mm.

Figura 56. *Amaranthus squamulatus* (Andersson) B. L. Rob. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A–D, ilustrado de *Holm-Nielsen 2323* (AAU); E, de *Holm-Nielsen 2128* (AAU). La barra de escala para A = 1 cm; para B–E = 1 mm.

ferrocarril (*Biurrum* & *Biurrum* 6766, CTES). Se la ha citado como maleza de montes frutales, cultivos de maní y poroto (*Krapovickas* & *Schinini* 32484, CTES). Crece entre los 100 m y los 1800 m (*Peirano s.n.*, CTES) (Pedersen, 1994). Florece entre los meses de octubre y mayo.

Nombres vulgares. Ataco (*Capparelli* 54, LP; *Parodi* 11040, F), ataco blanco (*Luna* 636, CTES), yuyo colorado (*Aguirre* 352, CTES).

Usos. *Amaranthus standleyanus* es una planta forrajera natural valiosa en regiones áridas (Boelcke, 1981).

Discusión. *Amaranthus standleyanus* es una especie próxima a *A. crispus* por sus frutos indehiscentes y cinco sépalos espatulados en sus flores pistiladas, aunque *A. crispus* tiene: 1) hojas con sus márgenes ondulados; 2) pecíolos de 10 mm o menores, y 3) sépalos aplicados al fruto cuando este madura. Por su parte, *A. standleyanus* se caracteriza por presentar hojas poco o no onduladas en el margen, pecíolo mayor de 1.8 cm y sépalos reflejos.

Ejemplares examinados. ARGENTINA. **Buenos Aires:** Pdo. Saliqueló, Saliqueló, *A. L. Cabrera* 7503 (CTES, LP). **Catamarca:** Dep. Ambato, 2 km NNE de El Bolsón, *C. Saravia Toledo et al.* 13245 (CTES); Dep. Andalgalá, 35 km W de Andalgalá (Km. 1539 en la ruta a Belén), *P. Cantino* 727 (CORD); 14 km SE de Andalgalá, camino a la Cuesta de la Chilca, *P. Cantino* 765 (CORD); Río Villavil, 1 km arriba de Villavil, *P. Cantino* 489 (CORD); Dep. Belén, Belén, *A. L. Cabrera* 1083 (LP); Londres, *A. Capparelli* 54 (LP); Hualfín, 16 ene. 1934, *Peirano s.n.* (CTES); Dep. La Paz, el Río de la Dorada, *A. Brizuela* 954 dupl. p.p. (CTES). **Chaco:** Dep. 1° de Mayo, Colonia Benítez, *A. G. Schulz* 3861 (CTES). **Córdoba:** Dep. Capital, Córdoba, Parque Sarmiento, *M. Terribile* 635 (CTES); Dep. Colón, Sa. Chica, falda E, Qda. del Río Primero, *A. T. Hunziker* 7052 (CORD); Dep. Cruz del Eje, Cruz del Eje, *M. Villafañe* 173 (CTES); Dep. Pocho, Sa. de Pocho, falda O, Ruta 20, después del último túnel, *A. T. Hunziker* & *J. A. Caro* 13492 (CORD); falda O al pie de la falda al comenzar la subida, *A. T. Hunziker* 13629 (CORD); Dep. Punilla, La Falda, *M. Villafañe* 731 (CTES); Lago San Roque, *A. T. Hunziker* 5979, 5993 (ambos en CORD); Tanti, *A. P. Rodrigo* 2187 p.p. (LP); Dep. Río Cuarto, zona de Cuatro Vientos, *von Müller* 303 (CORD); Dep. Río Segundo, *Est. Exp. INTA Manfredi* 56 (CORD); *A. Krapovickas* 6654 (CORD); Dep. San Alberto, Sa. Grande, falda O entre Las Rabonas y Nono, *A. T. Hunziker* 11883 (CORD); Dep. San Javier, Sa. Grande, falda O, entre San Javier y Las Rosas, *A. T. Hunziker* 11468 (CORD); Dep. San

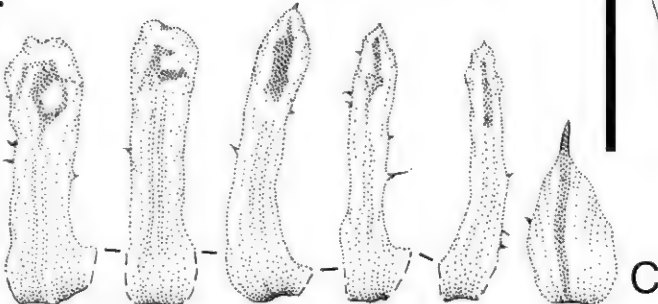
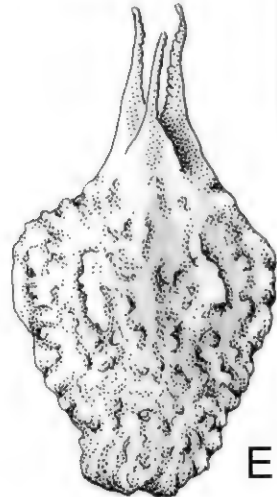
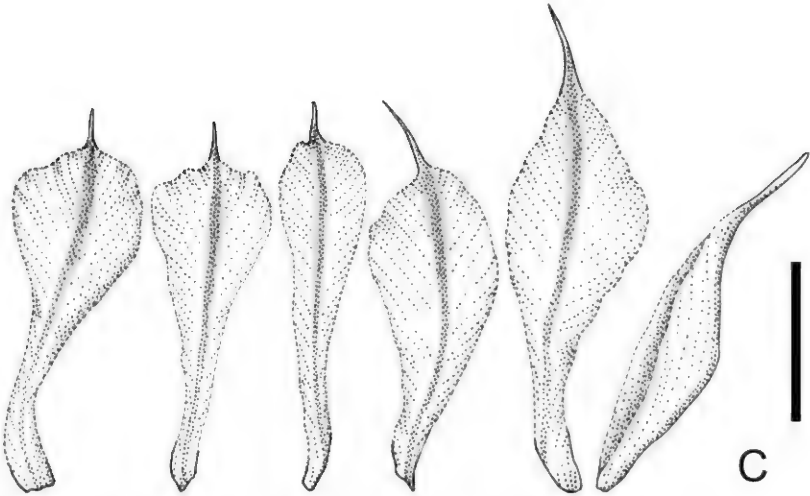
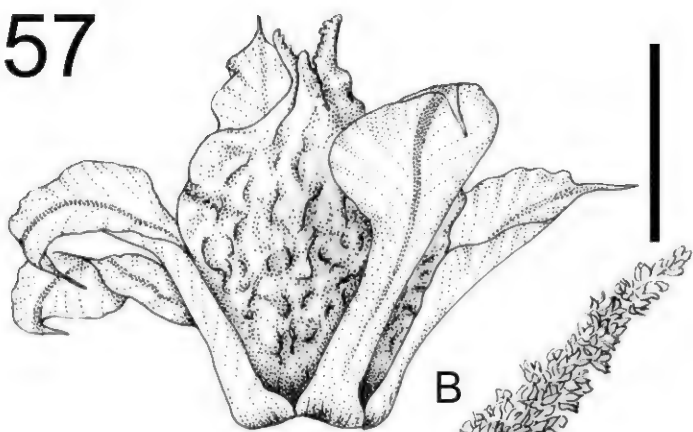
Justo, 13 km al E de la Francia, *A. Krapovickas et al.* 18522 (CTES); Dep. Santa María, Bajo Chico, ca. de Despeñaderos, *A. T. Hunziker* 6507 (CORD); Alta Gracia, *A. T. Hunziker* 491, 592 (ambos en CORD); Dep. Totoral, A. Macha, 5 km al O de Las Peñas, *A. T. Hunziker* 21835 (CORD); Dep. Tulumba, Salinas Grandes, entre San José y Km. 907 (antigua Salina Martorell), *A. T. Hunziker* & *R. Subils* 24595 (CORD); Dep. Unión, Canals, 20 abr. 1943, *R. Martínez Crovetto s.n.* (CORD). **Entre Ríos:** Dep. Concordia, Concordia, *R. Martínez Crovetto* & *Leguizamón* 4964 (SI). **Formosa:** Dep. Bermejo, Laguna Yema, *N. D. Bayón* & *C. A. Moreno* 717, 785 (ambos en LPAG); Dep. Patiño, Las Lomitas, *A. Schinini* & *S. M. Pire* 24189 (CTES). **Jujuy:** Dep. El Carmen, Pampa Blanca, *A. L. Cabrera et al.* 14246 (LP); Pampa Blanca, *A. L. Cabrera et al.* 23256 (CTES, LP); Dep. San Pedro, Cuesta de las Lajitas, *Cabrera et al.* 13786, 14404 (ambos en LP); San Juan de Dios, *O. Ahumada* & *A. Castellón* 4745 (SI); entre San Pedro y Santa Clara, *A. L. Cabrera et al.* 14622 (LP); Dep. Santa Bárbara, entre Santa Clara y Abra de los Morteros, *A. L. Cabrera et al.* 23354 (CTES, LP). **La Pampa:** Angoategui, *M. Birabén* 3021 (LP). **La Rioja:** Dep. Arauco, *A. T. Hunziker* 4972 (CORD); Aimogasta, *A. T. Hunziker* 4952 (CORD); Aimogasta, en el Río Aimogasta, *A. T. Hunziker* 5004, 5005 (ambos en CORD); Dep. Capital, camino entre La Rioja y La Ramadita, *A. T. Hunziker* 4796 (CORD); La Ramadita, a 25 km de La Rioja, *A. T. Hunziker* 4809 p.p. (CORD); Las Cañas, camino a El Cantadero, *A. T. Hunziker* 5054 (CORD); ciudad de La Rioja, *A. T. Hunziker* 4773 (CORD); estribación oriental de la Sa. de Velasco, El Cantadero, *A. T. Hunziker* 5296, 5135, 5137 (los tres en CORD); Cochangasta, *A. T. Hunziker* 5126 (CORD); Las Pederitas, camino al Dique de los Sauces, *A. T. Hunziker* 4834, 4838 (ambos en CORD); alr. de La Rioja, *G. Covas* 1121, 1136, 1141, 1148 (los cuatro en LP); Ruta Prov. 25 entre Punta Los Llanos y La Rioja, Ea. La Chilca, *F. Biurrum* & *L. Blanco* 7370 (CTES); Dep. Chilecito, Los Sarmientos, mar. 1990, *J. Rexach s.n.* (CORD); Chilecito, *G. Covas* 1181, 1186 (ambos en LP); faldeo O de la Sa. del Velasco, frente a Anguinán, *F. Biurrum et al.* 7026 (CTES); Dep. Castro Barros, entre Pinchas y Aminga, *A. T. Hunziker* 4933 (CORD); Dep. Famatina, Famatina, *T. M. Pedersen* 15300 (CTES); Dep. Gdor. Gordillo, llanos de La Rioja, límite E de Salina la Antigua, *A. T. Hunziker*, *A. E. Cocucci* & *J. A. Caro* 14363, 14381 (ambos en CORD); Ruta Nac. 38, entre Chamical y Chañar, Campo Exp. Las Vizcacheras, *F. Biurrum* & *C. Agüero* 1721 (CORD); Ruta Nac. 79, entre Camila y Casa de Piedra (Catamarca), Ea. Santa Josefa, *F. Biurrum* & *L. Blanco* 7382 (CTES); Chamical, *F. Biurrum* & *E. Biurrum* 6766 (CTES); entre Salina La Antigua y Casa de Piedra, Campo Exp. Los Cerrillos INTA, *E. Aguirre* 352 (CTES); Dep. Grl. Ocampo, Ruta 79, 1 km antes de Ambil al ir desde Tello, *A. T. Hunziker et al.* 14040 (CORD); a 2 km de Olpas, rumbo al empalme con Ruta Prov. 31, *Montes de Oca et al.* 722 (CORD); Dep. Gral San Martín, Bajo Hondo, Ea. El Tala, *D. L. Anderson* 3097 p.p. (CORD); Dep. Independencia, por Ruta 38, rumbo a La Rioja, 1–2 km N de Patquía, *A. T. Hunziker* 24669 (CORD); Dep. Sanagasta,

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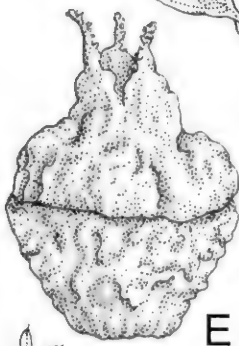
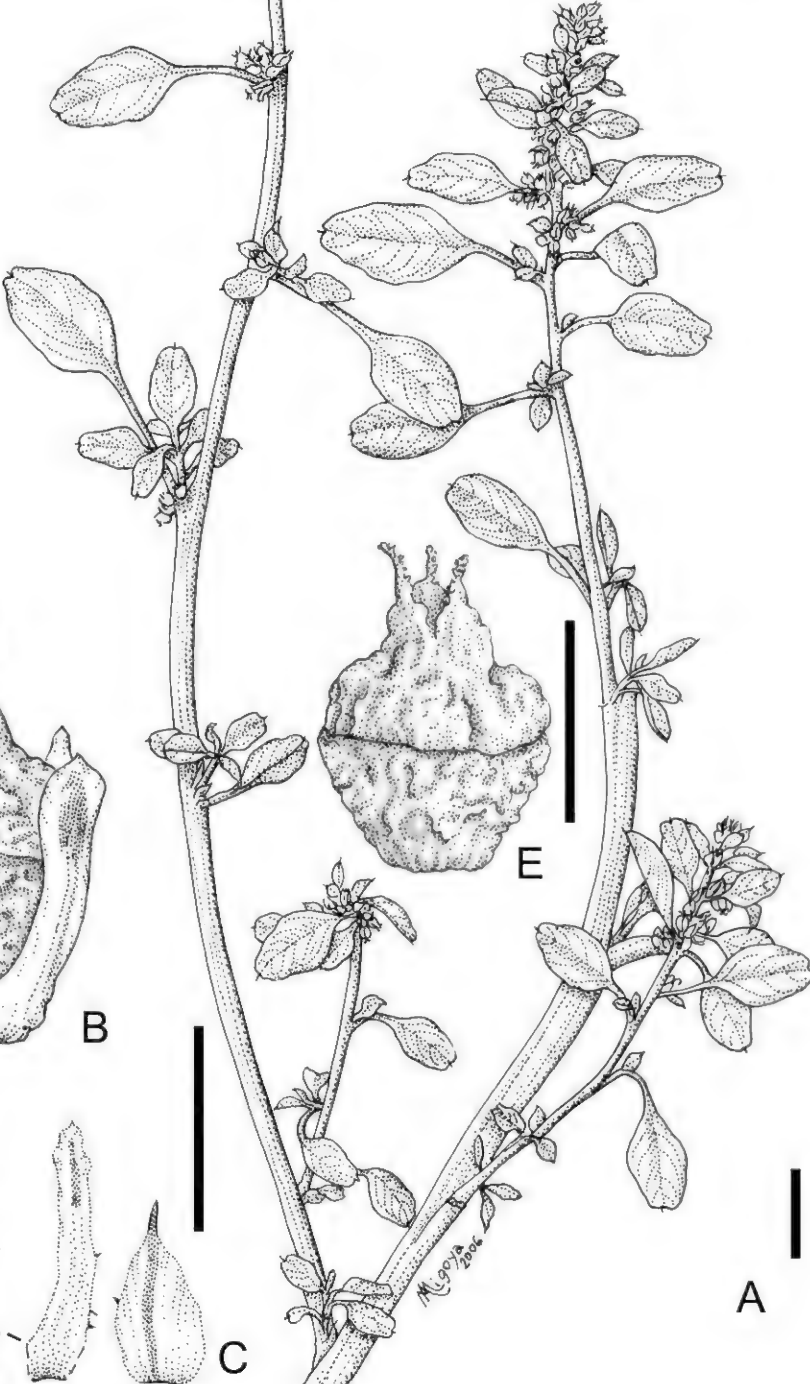
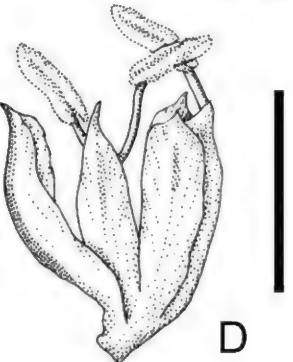
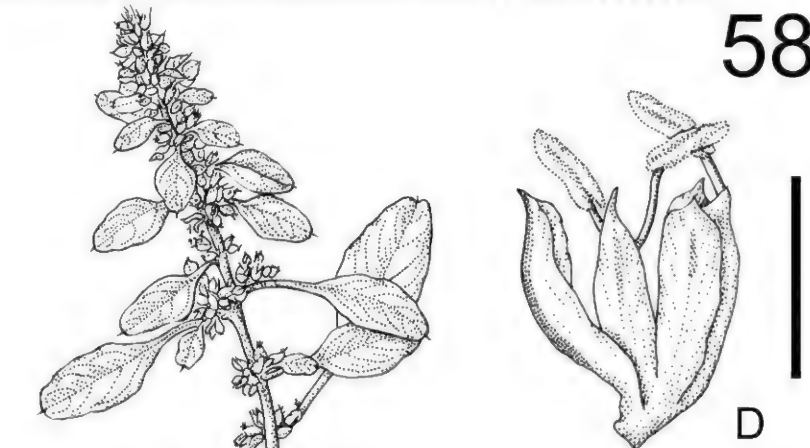
Figura 57. *Amaranthus standleyanus* Covas. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A, ilustrado de *Novara* 3413 (LP); B, de *Spegazzini* 167 (Z); C–E, de *Ahumada* & *Castillón* 4745 (SI). La barra de escala para A = 1 cm; para B–E = 1 mm.

Figura 58. *Amaranthus tamaulipensis* Henrickson. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A–E, ilustrado de *Duke* M3706 (MO). La barra de escala para A = 1 cm; para B–E = 1 mm.

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Dique Los Sauces, *A. T. Hunziker* 4714 (CORD); Sanagasta, *A. T. Hunziker* 4737, 4749, 4750, 4768 (los cuatro en CORD). **Mendoza:** Dep. San Rafael, San Rafael, *H. A. Lagiglia* 1440 (LP); s. loc., 1916, *E. Carette s.n.* (LP-22561, LP-22562); Dep. Santa Rosa, alr. de Ñacuñán, *F. Biurrun & Pagliari* 58 (CORD). **Salta:** Dep. Anta, *T. E. Luna* 153 (BA); Vinal Pozo, *F. E. Luna* 636 (CTES); Dep. Cafayate, Cafayate, dic. 1896, *C. L. Spegazzini s.n.* (LP); Dep. Cerrillos, finca El Rodeo, 6 km S de La Merced, *L. J. Novara* 3413 (LP); Dep. Grl. Güemes, *C. A. O'Donnell* 2642 (CTES); Dep. La Viña, Qda. de las Conchas, *A. L. Cabrera* 23734 (LP); Dep. Orán, Carapará, finca Bernar, *D. Abbiatti & L. Claps* 304 (LP); Senda Hachada, *M. R. Malvárez* 459 (CTES); Dep. Rivadavia, Misión La Paz, *G. F. Scarpa* 605 (CTES); 1 km al E de Santa Victoria Este, *G. F. Scarpa* 477 (CTES). **San Juan:** Dep. Caucete, 10 km NW de Marayes, *F. Biurrun & L. Blanco* 7472 (CTES); Dep. Sarmiento, ca. Villa Media Agua, *T. M. Pedersen* 11755 (CTES); Dep. Ullún, Qda. de las Burras, *T. M. Pedersen* 15218 (CTES); Dep. Valle Fértil, entre Ischigualasto y San Agustín del Valle Fértil, *F. A. Roig* 7823 (CORD); entre Marayes y Chucuma, *T. M. Pedersen* 11770 (CTES); sin dep. det., Co. Salinas, *E. Mauri* 27 (LP); *C. L. Spegazzini s.n.* (LP). **San Luis:** Dep. Belgrano, Nogolí, *A. Castellanos* 25/677 (CORD); Sa. de las Quijadas, Qda. del Alambre, O de San Antonio, *A. T. Hunziker & A. E. Cocucci* 16358 (CORD); Ruta Nac. 147, entre San Luis y San Juan, El Valle, 4 km O de San Antonio, *A. T. Hunziker & A. E. Cocucci* 16428, 16367 (ambos en CORD); Dep. La Capital, Alto Pencoso, *A. T. Hunziker et al.* 23394 (CORD); Alto Pencoso, *Bruch & Carette* 24, 87 (ambos en LP); Dep. Pedernera, 15 km N de Justo Daract, Ea. El Amanecer, *D. L. Anderson* 3018 (CORD). **Santa Fe:** Dep. 9 de Julio, 20 km S de Tostado, *T. M. Pedersen* 14537 (CTES). **Santiago del Estero:** Dep. Atamisqui, Salinas Grandes, entre el Río Saladillo e Isla Verde, *A. T. Hunziker & T. E. Di Fulvio* 21281 (CORD); Dep. Choya, Frías, *A. T. Hunziker* 2523, 2525 (ambos en CORD); Dep. Guasayán, Puerta Chiquita, *B. Piccinini & C. A. Petetin* 3281 (BAB); Dep. Ojo de Agua, sobre Ruta 9, atravesando las Salinas Grandes, *A. T. Hunziker* 21498 (CORD); Ruta 9, atravesando las Salinas Grandes, entre el 49 y el Río Saladillo, *A. T. Hunziker* 21797 (CORD); Dep. Rivadavia, unos 10 km O de La Isleta, O-SO de Ceres, *A. T. Hunziker* 10420 (CORD). **Tucumán:** sin dep. det., ene. 1899, *C. L. Spegazzini s.n.* (LP). **BOLIVIA. Chuquisaca:** Luis Calvo, El Salvador, *J. Pensiero & D. Marino* 4338 (MO). **Tarija:** Dep. Gran Chaco, 30 km N de Yacuibá, campo de Tapia, 2 km E de la Ruta a Villa Montes, *A. Krapovickas & A. Schinini* 32484 (CTES). **PARAGUAY. Boquerón:** 7 km NO de Fortín Nueva Asunción, *A. Schinini & R. Palacios* 25699 (CTES); Parque Nacional Tte. Enciso, *A. Schinini & R. Palacios* 25745 (CTES).

DINAMARCA. København, Vabygade, 1 sep. 1976, *S. Grove s.n.* (CTES-379560).

II. 44. *Amaranthus tamaulipensis* Henrickson, *Sida* 18(3): 800. 1999. TIPO: México. Tamaulipas: 13 mi. N of Aldama on rd. to Soto la Marina, 25 sep. 1960, *M. C. Johnston & J. Crutchfield* 5698 (holotipo, TEX [código de barras] TEX00375763 no visto, imagen!). Figura 58.

Hierba anual; tallos principales erectos o ascendentes, algunas veces decumbentes, 15–30(60) cm, ramificados en la base, no ramificados o con ramas

espaciadas arriba, glabros, frecuentemente con tonalidades rojizas. Hojas con pecíolo de 3–15(–21) mm, glabras, lámina ovada, rómbico-ovada, ondulada, (5–)10–27 × (2–)5–11(–18) mm, cuneada en la base, adelgazándose gradualmente hacia el ápice, este obtuso a redondeado, emarginado, mucronado, margen blanquecino. Inflorescencias predominantemente axilares, 0.6 cm de ancho, o semejando una espiga terminal al aproximarse los glomérulos axilares; brácteas y bractéolas lanceolado-ovadas, 0.7–1.2(–1.4) mm, algo más cortas que los sépalos, membranáceas, con la vena media de color verde, ápice agudo. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con 4 o 5 sépalos oblongo-ovados, agudos o acuminados, 1.2–1.6 mm, con la vena media verde, 3(4) estambres. Flores pistiladas con 5 sépalos oblongo-espatulados, 1.1–1.6(–2.1) mm, subiguales, separados, no superponiéndose excepto donde se expanden, lámina escariosa, unidos en la base, obtusos a redondeados; estigmas 3, anchos, cónicos, ± 0.2–0.3 mm. Frutos dehiscentes, 1.5–1.7 mm, más largos que los sépalos, enteramente rugoso-tuberculados, con costillas longitudinales, con un rostro patente, 0.3–0.5 mm, liso, inflado; semillas de color negro a castaño-rojizo, 1–1.2 mm, brillantes sobre todo en el área central.

Distribución y ecología. *Amaranthus tamaulipensis* se distribuye en los Estados Unidos de América (Texas) y México (San Luis Potosí, Tabasco y Tamaulipas). Se encuentra con frecuencia al costado de rutas y puede presentarse como maleza de cultivos (*King* 4056, US). Crece entre el nivel del mar y los 100 m (Mosyakin & Robertson, 2003). Florece y fructifica en los meses de septiembre, abril y marzo.

Discusión. *Amaranthus tamaulipensis* es una especie que podría confundirse con *A. dubius* de la que se puede distinguir porque esta última presenta sépalos con los márgenes membranáceos, más largos que el fruto, algo superpuestos y libres en la base, mientras que *A. tamaulipensis* presenta sépalos escariosos, algo más breves que el fruto, no superpuestos y unidos en la base.

Ejemplares examinados. MÉXICO. **San Luis:** San Luis Potosí, ca. El Salto arriba de El Naranjo, 6 abr. 1960, *J. A. Duke* M3760 (isoparatipo, *A. tamaulipensis*, MO). **Tamaulipas:** 2 mi. al NE de Altamira, *R. M. King* 4056 (US).

II. 45. *Amaranthus thunbergii* Moq. in de Candolle, *Prodr.* 13(2): 262. 1849, nom. reemplazo. Sin. reemplazado: *Amaranthus albus* Thunb., *Prodr.* Pl. Cap. Sch. 1: 215. 1794, non *Amaranthus albus* L., *Syst. Nat.* (ed. 10) 2: 1268. 1759. TIPO: Sudáfrica. “*Amaranthus albus* α, in cultis

Cap. b. Spei. Thunberg”, *Thunberg* 22237 (lectotipo, designado por Bayón y Freire [2011: 174], UPS no visto, imagen!). Figura 59.

Hierba anual; tallos principales decumbentes o erectos, 0.15–1 m, simples o \pm ramificados, especialmente abajo y a menudo en toda su longitud, con pelos largos y crespos cuando jóvenes, volviéndose glabrescentes a la madurez. Hojas con pecíolo de hasta 5 cm, glabras o glabrescentes a lo largo de la venación primaria en la cara abaxial, lámina obovado-elíptica a obovada o espatulada, no ondulada, 1–4(–5) \times (0.6–)1–3 cm, atenuada a cuneada en la base, obtusa, redondeada o retusa en el ápice, con mucrón de 0.5 mm. Inflorescencias axilares, en glomérulos de 6–10 mm diám, de color verde, que se hacen más próximos hacia el ápice de los tallos, dando inflorescencias terminales foliosas; brácteas y bractéolas deltoide-lanceoladas, 1.8–3 mm, por lo general más cortas que los sépalos, o raramente igualando o apenas excediéndolos en longitud, membranáceas, con una arista erecta o refleja de 0.5–1 mm. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con 3 sépalos lanceolados a oblongos, 2.5–5 mm (con la arista), aristados, 3 estambres. Flores pistiladas con 3 sépalos lanceolados a ovado-oblongos, 2.5–5 mm, desiguales, con la vena media de color verde, no ramificada, \pm reflejos, adelgazándose en una larga arista de 0.75–2 mm; estigmas tres, 0.5–1 mm, reflejos. Frutos dehiscentes, con el opérculo rugoso, urna lisa, con un corto rostro, más cortos que los sépalos; semillas de color negruzco, 1–1.5 mm diám, algo brillantes, finamente reticuladas.

Distribución y ecología. *Amaranthus thunbergii* es nativa de África tropical, desde Etiopía y Somalia hasta la República Democrática del Congo, y hacia el sur en Angola, Botswana, Namibia y Sudáfrica (Brenan, 1981). Introducida en Europa como planta ocasional en lugares donde se procesa la lana. En África se la encuentra en suelos lateríticos, pastoreados y en praderas adyacentes a ríos (*Dyson-Hudson* 182, US). También ha sido citada como maleza en jardines (*Parker* 3480, NBG) (Brenan, 1981). Florece entre los meses de noviembre y abril.

Nombre vulgar. Thunberg’s amaranth (Mosyakin & Robertson, 2003).

Discusión. *Amaranthus thunbergii* es una especie semejante a *A. tricolor* (asiática) por sus brácteas y bractéolas más cortas que los sépalos, los que son aristados en las flores pistiladas, con arista de al menos 0.75 mm. Se diferencian porque *A. tricolor* se trata de una planta cultivada de hojas e inflorescencias

con coloraciones vistosas (las últimas a menudo no foliosas) y porque tiene los sépalos de las flores pistiladas ensanchados en la mitad superior, mientras que *A. thunbergii* es una planta silvestre, sin coloraciones vistosas en las hojas ni en las inflorescencias, siendo estas siempre foliosas y con los sépalos más anchos en la mitad inferior. Se distingue de *A. dinteri* (especie africana afín) porque *A. thunbergii* tiene pelos largos en los tallos jóvenes y las aristas de los sépalos en las flores pistiladas de 0.75–2 mm, mientras que *A. dinteri* es subglabra cuando joven o a lo sumo tiene pelos rectos y cortos o papiliformes y sépalos con acumen de 0.1–0.5(–0.75) mm. *Amaranthus thunbergii* tiene los sépalos con la vena media de color verde no ramificada, careciendo por completo del sistema de ramificaciones que *A. dinteri* tiene en la mitad superior.

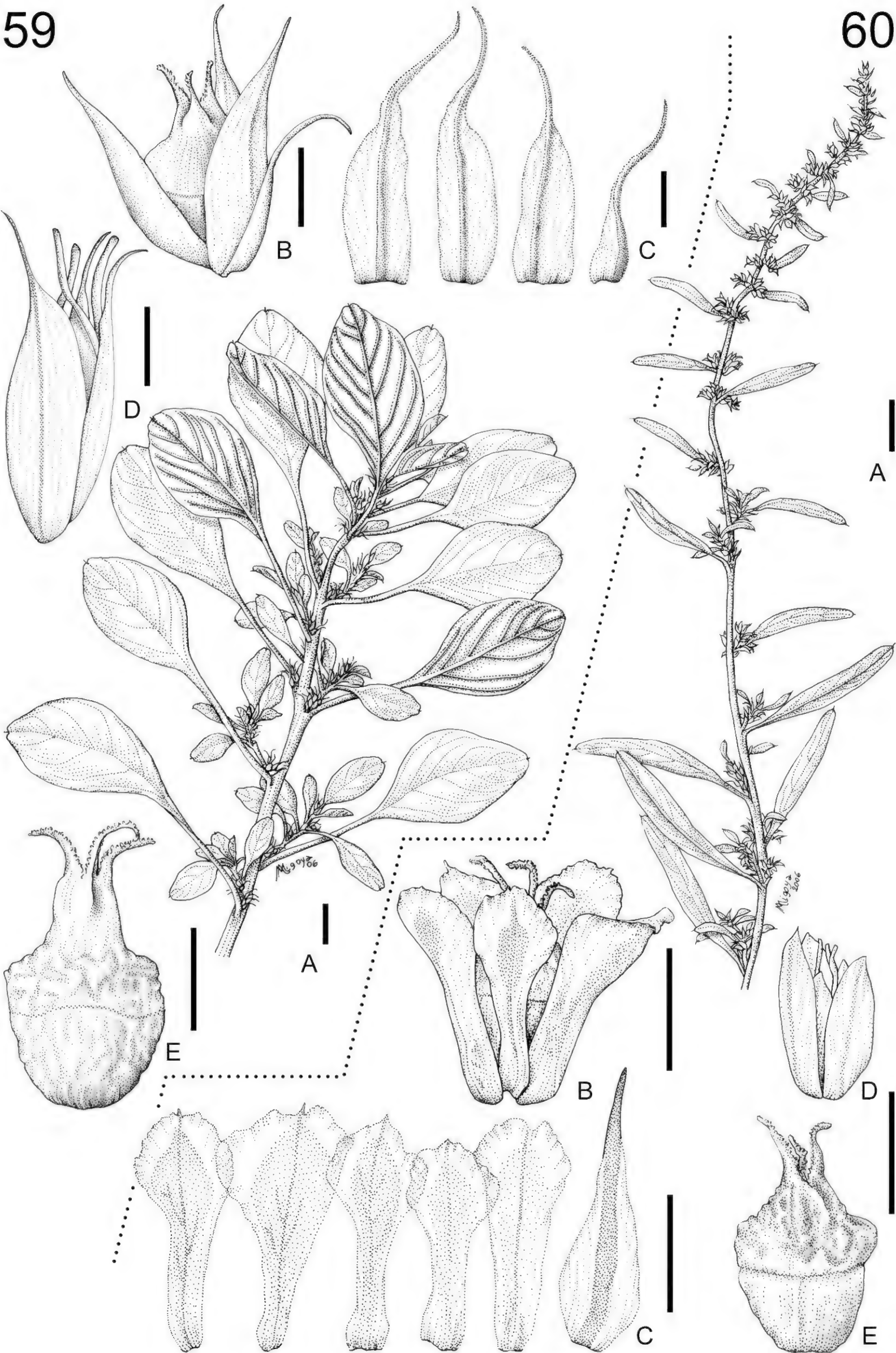
Ejemplares examinados. BOTSWANA. **Kgatlang:** Mochudi, Bechuanaland Protectorate, *C. C. Harbor* 6442 (US). NAMIBIA. **Ovamboland:** Ohopoho (Opuwo), 13°50'E, 18°4'S, *G. D. Gibson* 208 (US). SUDÁFRICA. **West Cape:** Stellenbosch, Devon Valley, *P. Nel & C. Boucher* 34 (NBG); Stellenbosch, Somerset West, *R. N. Parker* 3480 (NBG); Stellenbosch, Jonkenhaek, *R. N. Parker* 4559 (NBG); *K. L. P. Zeyher s.n.*, p.p. (NBG). UGANDA. **Karamoja:** near Emoruanaberru, *Dyson-Hudson* 182 (US).

ALEMANIA. Niedersachsen. Dohrener Wollwascherer lev Hannover, *R. Scheuermann s.n.* (US-865243).

II. 46. *Amaranthus torreyi* (A. Gray) Benth. ex S. Watson, Bot. California [W. H. Brewer] 2: 42. 1880. Basónimo: *Amblogyna torreyi* A. Gray, Proc. Amer. Acad. Arts 5: 167, 169. 1861, nom. reemplazo, como “*Amblogyne (Sarratia) Torreyi*”. Sin. reemplazado: *Sarratia berlandieri* Moq. var. *emarginata* Torr., Bot. Mex. Bound. 2(1): 179. 1859. *Amaranthus bigelovii* Uline & W. L. Bray var. *emarginatus* (Torr.) Uline & W.L. Bray, Bot. Gaz. 19: 271. 1894. TIPO: Estados Unidos de América. Texas: Brewster Co., Camp Green, en algún lugar entre Lajitas y Boquillas Canyon, oct. 1852, *C. C. Parry s.n.* (holotipo, NY [código de barras] NY01043123 no visto, imagen!; isotipos, NY [cb] NY01043124 no visto, imagen!, GH [cb] GH00037022 no visto, imagen!). Figura 60.

Amaranthus bigelovii Uline & W. L. Bray, Bot. Gaz. 19(7): 271. 1894, como “*Bigelovii*”. TIPO: Estados Unidos de América. Mtns. of the Río Cibola of the Río Grande, 18 ago. 1852, *Bigelow* 1190 (lectotipo, aquí designado, NY [código de barras] NY01043126 no visto, imagen!).

Amaranthus chihuahuensis S. Watson, Proc. Amer. Acad. Arts 21(2): 436. 1886, syn. nov. TIPO: México. Chihuahua: SW Chihuahua, hacienda San Miguel, ago.-sep. 1885, *E. Palmer* 197 (holotipo, GH [código de barras] GH00037024 no visto, imagen!; isotipos, K



[cb] K000582935 no visto, imagen!, NY [cb] NY00324454!, NY [cb] NY00324455!, PH [cb] PH00002340, US [cb] US00106240 no visto, imagen!, US [cb] US001062410 no visto, imagen!).

Amaranthus pringlei S. Watson, Proc. Amer. Acad. Arts 22(2): 476. 1887. TIPO: México. Chihuahua: Hills near Chihuahua, 26 sep. 1886, C. G. Pringle 795 (holotipo, GH [código de barras] GH00037029 no visto, imagen!; isotipos, AC [cb] AC00312953 no visto, imagen!, BR [cb] BR0000006950453 no visto, imagen!, COLO [cb] COLO00342386 no visto, imagen!, E [cb] E00296887 no visto, imagen!, F [cb] F0047591F no visto, imagen!, GOET [cb] GOET000080 no visto, imagen!, IBUG [cb] IBUG0179255 no visto, imagen!, LE [cb] LE00001703 no visto, imagen!, LL [cb] LL00370683 no visto, imagen!, MEXU [cb] MEXU00011550 no visto, imagen!, MICH [cb] MICH1115702 no visto, imagen!, MIN [cb] MIN1000115 no visto, imagen!, MSC [cb] MSC0129875 no visto, imagen!, NA [cb] NA0026074 no visto, imagen!, NDG [cb] NDG15512 no visto, imagen!, NY [cb] NY00324459!, NY [cb] NY00324460!, NY [cb] NY00324461 no visto, imagen!, P [cb] P00609935, no visto, imagen!, P [cb] P00609936 no visto, imagen!, PH [cb] PH00002350 no visto, imagen!, US [cb] US00106257 no visto, imagen!, US [cb] US00106258 no visto, imagen!, US [cb] US00106259 no visto, imagen!).

Hierba anual; tallos principales ascendentes a erectos, 10–70 cm, ramificados, glabrescentes a escasamente pubescentes. Hojas con pecíolo de hasta 1 cm, glabras, lámina de forma variable: oblongo-lanceolada, lanceolada u ovada, no ondulada, 1.5–5 × 0.3–2 cm, atenuada a cuneada en la base, aguda u obtusa en el ápice, con mucrón de 0.7 mm. Inflorescencias principalmente axilares, las que pueden presentarse agregadas en inflorescencias espici-formes carentes de hojas hacia el ápice; brácteas y bractéolas angustiovas, lanceoladas o lineares, (1.0–) 1.3–2.5 mm, iguales o algo mayores que los sépalos, con la vena media conspicua, verdosa, espinescente hacia el ápice. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con 4(5) sépalos lanceolados u oblongos, 2 mm, agudos u obtusos, 3 a 5 estambres. Flores pistiladas con 5 sépalos espatulados a angostamente espatulados, 1.5–2.5 mm, adelgazados en una uña en la mitad inferior, esta porción endurecida, con la vena media verdosa y ramificada, expandidos en un ala membranácea y refleja, obtusos, redondeados o retusos en el ápice, a veces con mucrón de hasta 0.3 mm; estigmas tres, 0.6–0.8 mm, delgados, erguidos. Frutos dehiscentes, con el opérculo rugoso, urna algo rugosa a lisa, igual o más breve que los

sépalos; semillas de color rojizo a negro, 1 mm diám, brillantes en el área central y punteadas y más opacas en la marginal.

Distribución y ecología. *Amaranthus torreyi* es característica del sudoeste de Estados Unidos de América y México. Prefiere los suelos arenosos o rocosos, en planicies o pendientes de grava. Crece entre los 1000 m y los 1700 m (Mosyakin & Robertson, 2003).

Nombres vulgares. Bigelow's amaranth, Torrey's amaranth, sandhill amaranth (Mosyakin & Robertson, 2003).

Discusión. *Amaranthus torreyi* es una especie muy próxima a *A. fimbriatus* y *A. obcordatus* por sus hojas delgadas, sus inflorescencias en espigas terminales no (o apenas) ramificadas y los sépalos de las flores pistiladas espatulados o flabelados y adelgazados en una uña basal. *Amaranthus fimbriatus* presenta el borde de los sépalos de sus flores pistiladas fimbriado o denticulado, no entero como en *A. torreyi*, y *A. obcordatus* tiene frutos indehiscentes, no dehiscentes como en *A. torreyi*.

Esta especie fue descrita originalmente por Torrey en Emory (1859) como *Sarratia berlandieri* var. *emarginata* sobre la base del ejemplar Parry s.n. Posteriormente, Gray (1861: 169) le asigna un nuevo status bajo el nombre de *Amblogyna torreyi*, mencionando como material estudiado el perteneciente a cuatro colectores: “On the Mexican border from the Rio Grande (Dr. Bigelow, Dr. Parry, etc.) to Lower California, Xantus, supra no. 100. A variety with linear or oblong-linear leaves and virgate spikes was collected near the sources of the Nebraska, by Mr. Henry Engelmann”. Esto corresponde a cuatro materiales de herbario, a saber: *J. M. Bigelow 1190* (GH, NY, US), *C. C. Parry s.n.* (GH, NY), *L. J. Xantus 100* (GH, NY, US) y *Engelmann s.n.* (GH, MO). Los especímenes *Bigelow 1190* y *Parry s.n.* son monoicos (pese a que Gray habla de plantas dioicas en la descripción). Uline y Bray (1894) describen *Amaranthus bigelovii* (sobre la base del ejemplar *Bigelow 1190*) y proponen la nueva combinación: *Amaranthus bigelovii* Uline & W. L. Bray var. *emarginatus* (Torr.) Uline & W. L. Bray (\equiv *Sarratia berlandieri* Moq. var. *emarginata* Torr.) sobre la base

←
Figura 59. *Amaranthus thunbergii* Moq. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A, C, ilustrado de Dyson-Hudson 182 (US); B, D, E, de Harbor s.n. (US). La barra de escala para A = 1 cm; para B–E = 1 mm.

Figura 60. *Amaranthus torreyi* (A. Gray) S. Watson. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A–E, ilustrado de Pringle 795 (NY). La barra de escala para A = 1 cm; para B–E = 1 mm.

del ejemplar *Parry s.n.* Por su parte, los especímenes *Xantus 100* y *Engelmann s.n.* no pertenecen a *Amaranthus torreyi*, sino a dos amarantos dioicos: *Amaranthus watsonii* Standl. y *Amaranthus arenicola* I. M. Johnston, respectivamente.

Finalmente, Watson (1880) propone la nueva combinación *Amaranthus torreyi* sin citar material alguno, ni aludir a la monoecia o dioecia de la especie. Dado que el ejemplar de *Parry s.n.* fue asociado desde un principio a este taxón, (como se observa en la descripción original de Torrey de 1859) se entiende que debe ser considerado como el holotipo de *A. torreyi*, eligiéndose al ejemplar NY-1043124 por presentar una planta completa, que se corresponde con la diagnosis original.

Amaranthus bigelovii fue descrito por Uline y Bray (1894a: 271) sobre la base del ejemplar *Bigelow 1190*. En la diagnosis original los autores mencionan el lugar y año de colección: “Mountains of the Cibola in 1852”. Ha sido posible detectar cuatro especímenes que responden al protólogo: US-00106233, NY-01043125, NY-01043126 y GH-00037031. El ejemplar de US, si bien lleva el número 1190, carece de lugar y fecha de colección. De los especímenes depositados en NY, el primero de ellos (NY-01043125) presenta en su etiqueta el número de colección 1190, sin lugar ni fecha, mientras que el segundo (NY-01043126) tiene las siguientes leyendas en su etiqueta: “Mountain on the Cibola of the Rio Grande”, y “Aug. 18/52”, aunque carece de número de colección. Finalmente, la cartulina del GH consta tan solo de fragmentos de hojas e inflorescencias. Tomando todo lo antedicho en consideración, se designa al ejemplar NY-01043126 como lectotipo de *A. bigelovii* dado que se trata de un ejemplar bien conservado, que se ajusta a la descripción y a los datos que aparecen en el protólogo.

Mosyakin y Robertson (2003) vinculan a *Amaranthus chihuahuensis* con *A. fimbriatus*, pero afirman que su identidad taxonómica permanece oscura. Se ha estudiado el material tipo de *A. chihuahuensis*, correspondiente a los ejemplares *E. Palmer 197* depositados en GH, K, NY, PH y US, en los que se observa que tanto la morfología de sus inflorescencias, como la de sus flores y frutos son muy semejantes a las de *A. torreyi*, de la que se considera sinónimo.

Ejemplares examinados. ESTADOS UNIDOS DE AMÉRICA. **Nuevo México:** Mtns. de Cibola, 1852, *J. M. Bigelow 1190* (sintipo, *Amaranthus bigelovii*, US-00106233); Mtns. of the Cibola of the Rio Grande, 18 ago. 1852, *J. M. Bigelow 1190* (sintipo, *A. bigelovii*, GH-00037031, fragm.). **Texas:** Mtns. de Cibola, Presidio Co., 18

ago. 1952, *J. M. Bigelow 1190* (sintipo, *A. bigelovii*, NY-01043125).

II. 47. *Amaranthus tricolor* L., Sp. Pl. 2: 989. 1753.
TIPO: [India.] “Habitat in India”, *Herb. Linnaeus 1117.7* (lectotipo, designado por Townsend [1974a: 14], LINN 1117.7 no visto, imagen!). Figura 61.

Amaranthus melancholicus L., Sp. Pl. 989. 1753. TIPO: [India.] “Habitat in India”, *Herb. Linnaeus 1117.4* (lectotipo, designado por Townsend [1994: 11], LINN 1117.4 no visto, imagen!).

Amaranthus tristis L., Sp. Pl. 989. 1753, non *Amaranthus tristis* Willd., Hist. Amaranth. 21. 1790. *Amaranthus tricolor* L. var. *tristis* (L.) Thell., Syn. Mitteleur. Fl. 5(Abth. 1): 267. 1919. TIPO: [China.] “Habitat in China”, *Herb. Linnaeus 1117.11* (lectotipo, designado por Iamónico [2014a: 149], LINN 1117.11 no visto, imagen!).

Amaranthus mangostanus L., Cent. Pl. I: 32. 1755. TIPO: [India.] “Habitat in India”, *Herb. Linnaeus 1117.10* (lectotipo, designado por Iamónico [2014a: 147], LINN 1117.10 no visto, imagen!).

Amaranthus polygamus L., Cent. Pl. I: 32. 1755. TIPO: [India.] “Habitat in India”, *Herb. Linnaeus 1117.9* (lectotipo, designado por Iamónico [2014a: 148], LINN 1117.9 no visto, imagen!).

Amaranthus inamoenus Willd., Sp. Pl. ed. 4 [Willdenow] 4(1): 386. 1805. TIPO: Japón, *C. L. Willdenow 17504* (holotipo, B [código de barras] BW17504-010 no visto, imagen!).

Hierba anual; tallos principales ascendentes a erectos, de hasta 1.5 m, robustos, a menudo ramificados, angulares, glabros o pubescentes principalmente cerca de la inflorescencia. Hojas con pecíolo de hasta 6.5 cm, glabras o glabrescentes, lámina de forma variable, ovada, rómbica, elíptica o lanceolada, no ondulada, 3–15 × 1.5–6.5 cm, atenuada a cuneada en la base, emarginada u obtusa en el ápice, mucronada, con el margen entero, de color verde, a veces con tintes purpúreos. Inflorescencias axilares, en glomérulos de 10–25 mm diám, de color verde a rojizo, distantes en la base de los tallos y próximos en el ápice donde a menudo carecen de hojas, resultando en una pseudoespiga terminal de tamaño variable; brácteas y bractéolas ampliamente deltoide-ovadas, de hasta 3.7 mm, menores o casi de la misma longitud que los sépalos, membranáceas, con una base amplia que va adelgazándose gradualmente hacia el ápice, pálidas, ápice con arista de 0.5–1.1 mm, recta o curva. Flores de ambos sexos sobre la misma inflorescencia. Flores estaminadas con 3 sépalos obovado-lanceolados o lanceolados, 3–5.6 mm, 3 estambres. Flores pistiladas con 3 sépalos lanceolados, ovados o elípticos, 3–5 mm, pálidos, membranáceos, anchos en la base, adelgazándose gradualmente hacia el ápice, con una arista 0.5–0.75 mm, recta o curva; estigmas tres,

0.75–1.2 mm, erectos o curvos. Frutos dehiscentes, rugosos, con un rostro marcado, más cortos que los sépalos; semillas de color castaño-negruzco, 1–1.2 mm diám, brillantes y lisas en el centro, reticuladas en el área marginal.

Distribución y ecología. *Amaranthus tricolor* es originaria de Asia, distribuyéndose en Pakistán, China, Japón y Filipinas por el norte, e Indonesia al sur. Ha sido introducida en África (Townsend, 1985, 1988) e Indias Occidentales (Fawcett & Rendle, 1914). Es una planta silvestre que puede constituirse en maleza (Townsend, 1980).

Nombres vulgares. Amaranto tampala (de la Peña & Pensiero, 2004); Joseph's coat, summer poinsettia (Mosyakin & Robertson, 2003).

Usos. *Amaranthus tricolor* es utilizada como hortaliza de hoja, siendo tan apreciada como la espinaca (*Spinacia oleracea* L., Amaranthaceae) en la región tropical de Asia (Sur de China) (*Shiu Ying Hu* 7857, US). Las formas purpúreas son apreciadas por su valor ornamental, siendo cultivada en áreas de poca altitud y secas, convirtiéndose a veces en maleza de jardines (*Wheeler* 12842, US). En Asia florece y fructifica en los meses de junio, agosto, enero y febrero.

Discusión. *Amaranthus tricolor* se asemeja a *A. thunbergii* por sus brácteas y bractéolas más cortas que los sépalos, los que son aristados en las flores pistiladas, con arista de 0.1 mm. Se diferencian porque *A. thunbergii* es una planta silvestre, sin coloraciones vistosas en las hojas ni en las inflorescencias, siendo estas siempre foliosas y con flores pistiladas con sépalos más anchos en su mitad inferior. Por su lado, *A. tricolor* es a menudo cultivada por las coloraciones vistosas de las hojas e inflorescencias, estas últimas a menudo no foliosas y con los sépalos de las flores pistiladas ensanchados en su mitad superior. Otras dos especies próximas son *A. albus* y *A. graecizans*, pues comparten con *A. tricolor* el número de tres sépalos en las flores pistiladas y los frutos dehiscentes. Sin embargo, *A. albus* tiene bractéolas mucho más largas que los sépalos (no más cortas como en *A. tricolor*) y *A. graecizans* posee los sépalos de menor longitud que el fruto (no mayor como en *A. tricolor*).

Ejemplares examinados. CHINA. **Hong Kong:** Shek Kong, *Shiu Ying Hu* 7857 (US). FILIPINAS. **Luzón:** Manila, Malate, *E. Fénix* 2-107 (US). **Palawan:** *J. Bermejos* 39771 (US). INDIA. **Bengala:** Calcuta, *J. W. Helfer* 37 (NY). SRI LANKA. **Central:** Gannouruwa, Kendy Distr., *L. C. Wheeler* 12842 (US). **Norte:** Mannar, *C. C. Townsend* 73/101 (US).

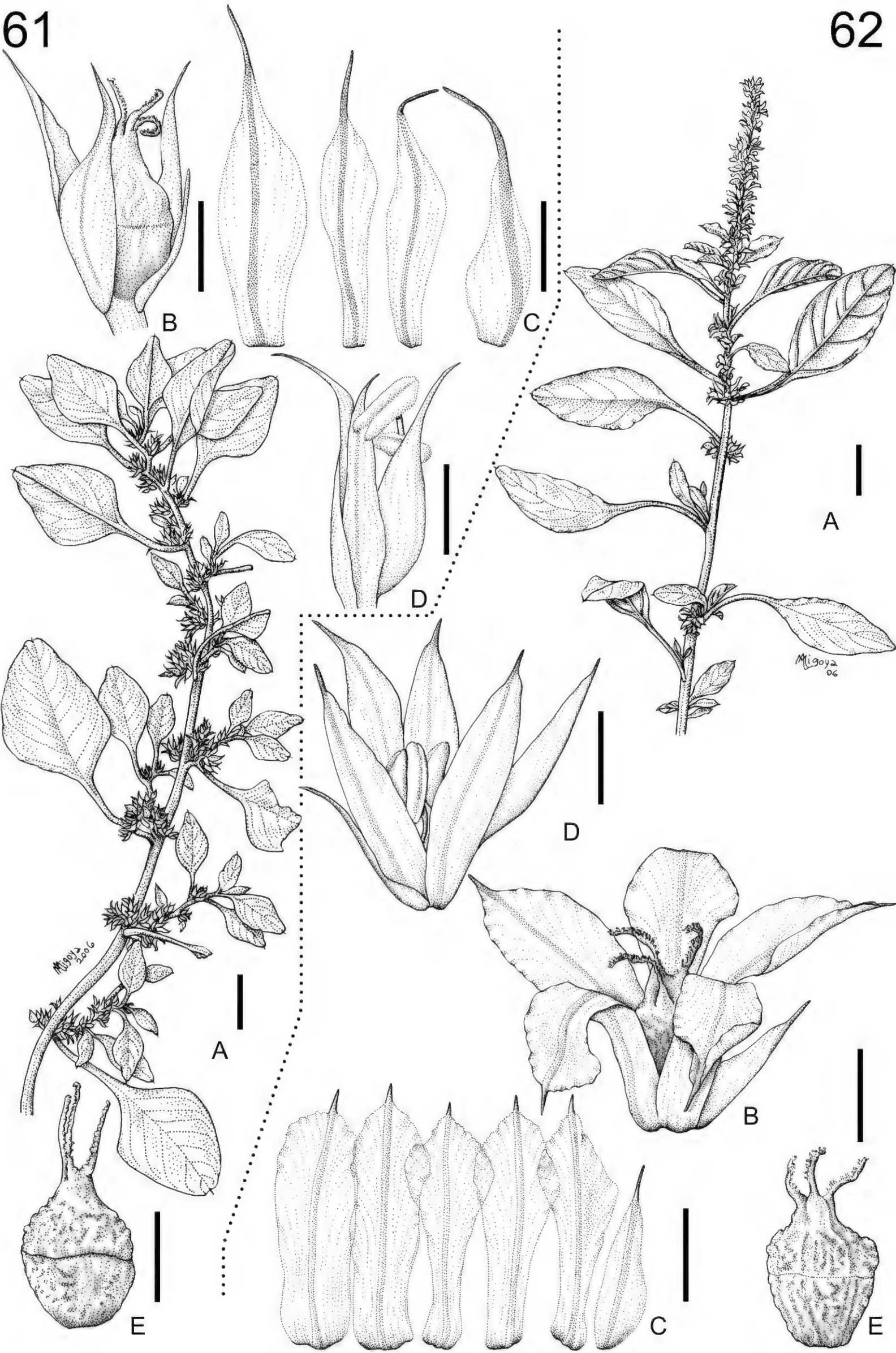
II. 48. *Amaranthus undulatus* R. Br., Prodr. Fl. Nov. Holland. 414. 1810. *Euxolus undulatus* (R. Br.) Moq. in de Candolle, Prodr. 13(2): 268, 272. 1849. TIPO: [Australia]. Arnhem N Bay [Melville Bay, Northern Territory], mayo 1802, *R. Brown* [Iter Australiense] 3047 (holotipo, BM p.p. [material fértil, un fragmento y una planta completa a la derecha] [código de barras] BM000522508 no visto, imagen!). Figura 62.

Amaranthus pallidiflorus F. Muell., Fragmenta Phytographiae Australiae 1(5): 140. 1859. TIPO: Australia. Northern Territory: en las orillas de cursos de agua entre los ríos Victoria y Fitzmaurice, Arnhem Aboriginal Land, oct. 1855, *F. Mueller* s.n. (holotipo, MEL-59733 no visto, imagen!).

Amaranthus leptostachyus Benth., Fl. Austral. 5: 214. 1870. TIPO: Australia. Queensland: "Two Isles" off Cape Flattery, 31 jul. 1848, *J. MacGillivray* s.n. (lectotipo, designado por Palmer [2009: 123], K no visto, imagen!; isoelectotipo, K no visto, imagen!).

Hierba anual; tallos principales decumbentes a erectos, 30–60 cm, simples o ramificados, glabros. Hojas con pecíolo de (0.5–)1–2.3 cm, glabras, lámina ovada, rómbica o trulada, algo ondulada, 0.5–4.5 × 0.3–3 cm, cuneada en la base, aguda a obtusa en el ápice, con mucrón de 0.2–0.6 mm, algo discolor, de color verde claro con venas marcadas y blanquecinas en la cara abaxial. Inflorescencias terminales y axilares, las primeras en espigas interrumpidas (a veces caudadas) que al reunirse conforman una panoja, 10–15 × 0.5–1 cm, erectas; las segundas en glomérulos; brácteas y bractéolas lanceoladas u ovadas, (0.75–)1.4–2.2 mm, más cortas que los sépalos, rara vez de la misma longitud, membranáceas con la vena media marcada, de color verde, excurrente y espinescente. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con 4 o 5 sépalos oblongo-lanceolados, 2.3–3.3 mm, mucrón 0.3 mm, 3 o 4 estambres. Flores pistiladas con 4 o 5 sépalos angostamente obovados a espatulados, 2.4–3 mm, a menudo recurvos, pálidos a casi blancuzcos, obtusos a redondeados en el ápice, escariosos, más largos que el fruto, con la lámina expandida, adelgazados en una uña en la base, vena media verdosa, delgada 0.1 mm ancho, ramificada, excurrente en un mucrón 0.3–0.5 mm; estigmas 3, delgados y abiertos, 0.75–1 mm. Frutos dehiscentes, pálidos, opérculo rugoso, con un rostro conspicuo y grueso de 0.6 mm; semillas de color castaño oscuro, 1.25 × 1 mm, finamente punteadas y brillantes en el centro, más opacas en el margen.

Distribución y ecología. *Amaranthus undulatus* es una especie propia del continente australiano, donde crece en las regiones de Pilbara y Kimberley (incluyendo las islas) de Western Australia, en las



inmediaciones del Río Victoria y del Golfo de Carpentaria del Northern Territory, cerca de los Montes Isa y Mulligan en Queensland y en las islas del Estrecho Torres (distribución tomada de Palmer, 2009). En Australia se la ha encontrado en floración entre los meses de marzo y julio.

Discusión. *Amaranthus undulatus* sería la única especie australiana que por sus rasgos morfológicos se aproxima a las especies de *Amaranthus* subg. *Amaranthus*. Como ya puntualizaran Mosyakin y Robertson (1996), esta especie es cercana a *A. mitchellii*, y el desarrollo de sus inflorescencias apicales sería el resultado de un caso de evolución paralela. *Amaranthus mitchellii* es una especie difícil de confundir con ninguna otra por sus frutos con costillas prominentes longitudinales y un rostro patente. Sus sépalos son espatulados y doblados hacia afuera, como en *A. undulatus*, pero en esta última especie se destacan las inflorescencias terminales. Además, sus frutos no tienen las citadas costillas, siendo además dehiscentes.

Ejemplares examinados. AUSTRALIA. **Northern Territory:** Northern Australia, Port Darwin, *Schultz s.n.* (paratipo, *Amaranthus leptostachyus*, MEL no visto, imagen!); South Bay, Bickerton Island, Golfo de Carpentaria, sobre una duna costera, *R. L. Specht 567* (NSW); Port Darwin, *M. W. Holtze 45* (MEL); Melville Isl., E de Brenton Bay, *I. D. Cowie 5526* (MEL). **Western Australia:** 3 km N de Silent Grove Homestead, *R. J. Cranfield 6532* (NSW); Gascoyne Ruien, *F. Mueller s.n.* (Z); entre los ríos Ashburton y De Gray, *E. Clement s.n.* (K); Wittenoom Gorge, Hammersley Ranges, *D. E. Symon 5395* (K); Río Fortescue ca. Balmoral, *D. E. Symon 5412* (K); Wilson Creek, 18.5 km al NO de Home Valley, Kimberley, *M. Lazarides 8628* (NSW).

II. 49. *Amaranthus urceolatus* Benth., Bot. Voy. Sulphur 158. 1844. *Sarratia urceolata* (Benth.) Moq. in de Candolle, Prodr. 13(2): 269. 1849. TIPO: Ecuador. Guayas: Guayaquil, Puna, *Sinclair s.n.* (holotipo, K [código de barras] K000190108 no visto, imagen!; isotipos, K [cb] K000591164 no visto, imagen!, P [cb] P05003005 no visto, imagen!). Figura 63.

Amaranthus haughtii Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 11(5): 149. 1936. TIPO: Perú. Piura: Pariñas Valley, 18 mar. 1929, *O. Haught F147* (holotipo, F-589332 no visto, imagen!).

Hierba anual; tallos principales erectos, algunas veces ascendentes, 15–80 cm, escasamente ramificados, glabros o con algunos pelos cortos, especialmente cerca de la inflorescencia. Hojas con pecíolo de 0.5–3 cm, glabras, lámina angostamente oblonda a ovado-elíptica, no ondulada, 1–4 × 0.25–2 cm, muy gradualmente atenuada a cuneada en la base, redondeada a levemente emarginada, con mucrón de 0.8–1 mm. Inflorescencias axilares, en glomérulos de 0.5–1 cm diám, reuniéndose hacia el ápice y dando origen a espigas terminales foliosas; brácteas y bractéolas lanceoladas a ovado-lanceoladas, 1 mm, a lo sumo alcanzando la longitud de los sépalos, membranáceas, con la vena media marcada, ápice agudo. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con 5 sépalos lanceolados a oblongo-lanceolados, 1–1.3(–1.6) mm, agudos, (2)3 estambres. Flores pistiladas urceoladas, con 5 sépalos espatulados, dos más anchos que los restantes en la mitad inferior, 1.3–2 mm, la mitad superior refleja, expandida, ápice redondeado a truncado; vena media de color verde, ramificada; los sépalos están engrosados y soldados en la base, más angostos en su tercio medio, permitiendo ver el ovario, entre ellos; cáliz expandido en flores plenamente desarrolladas llegando a tener 2 mm diám en la porción distal, generalmente más largo que el fruto, pero en algunos especímenes más breve; estigmas 3, ca. 0.5 mm, ensanchados en la base. Frutos indehiscentes (a veces con cierta tendencia a la dehiscencia), con la mitad superior rugosa y la inferior encerrada dentro del tubo del cáliz; semillas de color castaño-rojizo a negro, 0.7–0.9 × 0.8–1 mm, brillantes en el centro y punteadas en el margen.

Distribución y ecología. *Amaranthus urceolatus* habita Ecuador y Perú, prefiriendo suelos de lugares arenosos abiertos, aluvionales o en montes bajos subxerófilos (*Ferreira et al. 10572*, US; *López Miranda et al. 9185*, MO). También crece sobre formaciones rocosas altas junto al mar. Se encuentra hasta los 3600 m (Eliasson, 1987). Florece entre los meses de febrero y junio.

Discusión. *Amaranthus urceolatus* es una especie cercana a todas aquellas que presentan flores pistiladas urceoladas, como *A. anderssonii*, *A. hunzikeri*, *A. kloosianus*, *A. polygonoides* y *A. squamulatus*. De *A. anderssonii* y de *A. polygonoides*

Figura 61. *Amaranthus tricolor* L. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A–E, ilustrado de *Helpfer 37* (NY). La barra de escala para A = 1 cm; para B–E = 1 mm.

Figura 62. *Amaranthus undulatus* R. Br. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A, ilustrado de *Mueller s.n.* (Z); B–E, de *Symon 5395* (K). La barra de escala para A = 1 cm; para B–E = 1 mm.

se distingue por el número de estambres, dado que estas tienen sólo dos estambres y no generalmente tres, mientras que *A. kloosianus* presenta cinco estambres. *Amaranthus hunzikeri* tiene hábito postrado, hojas espatuladas y frutos dehiscentes, mientras que *A. urceolatus* tiene hábito erecto, hojas oblongas u ovadas y frutos indehiscentes. *Amaranthus squamulatus* es quizás la especie más cercana, pero presenta un diámetro distal de sus flores pistiladas de 3.5–5 mm mientras que en *A. urceolatus* es de 2 mm.

Ejemplares examinados. ECUADOR. **Guayas:** Entre Santa Elena y La Libertad, *E. Asplund* 5027, 5140 (ambos en US); 2°13'S, 81°W, *H. K. Svenson* 11280 (US); desde Libertad, ca. de Salinas, a 10 km al O a lo largo de la costa, *W. G. D'Arcy* 13728 (MO). **Manabí:** 12 km al N de Portoviejo, *B. MacBryde* 1045 (MO); La Plata Island, a 23 km de la costa, ca. 55 km SO de Manta, *L. B. Holm-Nielsen et al.* 7304 (AAU). PERÚ. **Cajamarca:** Contumazá, El Portachuelo de San Antonio, *A. López Miranda et al.* 9185 (MO). **Piura:** Pariñas Valley, 18 mar. 1929, *O. Haught* 221 (paratipo, *Amaranthus haughtii*, US), 227. **Tumbes:** entre Tumbes y Zarumilla, *R. Ferreyra et al.* 10572 (US).

II. 50. *Amaranthus viridis* L., Sp. Pl. ed. 2. 2: 1405. 1763. *Glomeraria viridis* (L.) Cav., Descr. Pl. 319. 1802. *Euxolus viridis* (L.) Moq. in de Candolle, Prodr. 13(2): 273. 1849. TIPO: “Habitat in Europa, Brasilia”, *Herb. Linnaeus 1117.15* (lectotipo, designado por Fawcett & Rendle [1914: 131], LINN 1117.15 no visto, imagen!). Figura 64.

Hierba anual o perenne de corta vida; tallos principales usualmente erectos, decumbentes o postrados, 15–60 cm, simples o ramificados en la base, glabros o algo pubescentes, especialmente cerca de la inflorescencia. Hojas con pecíolo de hasta 9 cm, glabras o pubescentes sobre la vena media de la cara abaxial, lámina ovada, ovado-elíptica o rómbica, no ondulada, 2–12 × 1.5–6 cm, ampliamente cuneada o raramente redondeada en la base, obtusa o redondeada en el ápice o someramente emarginada, mucronada. Inflorescencias terminales y axilares, las primeras delgadas, generalmente formando una espiga simple larga y delgada, de color verde, 2–16 × 0.4–0.8 cm, sin hojas en la porción distal, y las axilares en glomérulos de hasta 6 mm diám; brácteas y bractéolas ovado-deltoides, 0.4–1 mm, más cortas que los sépalos, membranáceas, con

la vena media de color verde. Flores de ambos sexos sobre una misma inflorescencia. Flores estaminadas con 3 sépalos ampliamente elípticos, 8–12 mm, 3 estambres. Flores pistiladas con 3 sépalos oblongos o angostamente espatulados, 0.8–1.6 mm, con la vena media gruesa y de color verde en la mitad superior, cortamente mucronados o sin mucrón; estigmas dos o tres, 0.25–0.4 mm. Frutos indehiscentes, casi iguales o apenas más largos que los sépalos, muy rugosos en toda su superficie; semillas de color castaño oscuro a negro, 1.1–1.3 mm diám, algo brillantes, reticuladas, finamente verrugosas.

Distribución y ecología. *Amaranthus viridis* es nativa de Sudamérica, aunque ampliamente naturalizada por todo el mundo, principalmente en regiones tropicales, subtropicales y en regiones templadas de América (Mosyakin & Robertson, 2003), Asia (Aellen, 1972; Townsend, 1974a; Bojian et al., 2003), Australia (Palmer, 2009) y Europa (Tutin & Edmonson, 1993). Es considerada una planta ruderal, común en suelos modificados, a veces convertida en maleza, que crece entre el nivel del mar y los 1500 m (Pedersen, 1994). Florece durante todo el año.

Nombres vulgares. Bledillo, bledo, caá-rurú, caá-rurú macho, chaclión, chaquillón, karurú, quinoa rosada, yerba del sapo (*Keller 2991*, CTES) (de la Peña & Pensiero, 2004); slender amaranth, tropical green amaranth, green amaranth (Mosyakin & Robertson, 2003).

Usos. Las hojas de esta especie son consumidas como hortaliza y a veces es empleada como medicinal (*Montes 10223*, LP).

Discusión. *Amaranthus viridis* es una especie semejante a *A. blitum* de la que se distingue por tener hojas a veces muy levemente emarginadas y flores pistiladas con tres o cuatro sépalos, mientras que *A. blitum* presenta hojas marcadamente emarginadas y flores pistiladas con dos o tres sépalos.

Amaranthus gracilis fue descrita por J. L. M. Poirét (1810: 312), en cuya diagnosis se la particulariza por sus tallos simples y erectos, hojas ovadas y obtusas, inflorescencias espigado-paniculadas y flores estaminadas con tres estambres. Por otra parte, no se hace

Figura 63. *Amaranthus urceolatus* Benth. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A–E, ilustrado de *Haught 221* (US). La barra de escala para A = 1 cm; para B–E = 1 mm.

Figura 64. *Amaranthus viridis* L. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A–E, ilustrado de *Bayón 613* (LPAG). La barra de escala para A = 1 cm; para B–E = 1 mm.



mención de material tipo, citándose la localidad “On la soupeonne originaire de la Guinée”. No ha sido posible localizar material tipo asociado a este nombre, que con frecuencia es empleado en lugar de *A. viridis* (Aellen, 1959; Maire, 1962; Carretero, 1979).

Ejemplares examinados. ARGENTINA. **Buenos Aires:** Pdo. Chacabuco, 1922, s. coll. (LP); Pdo. La Plata, *N. D. Bayón* 603, 1093 (ambos en LPAG); La Plata, *A. L. Cabrera* 5227, 10059 (ambos en LP); Los Hornos, *N. D. Bayón* 1329 (LPAG); Pdo. San Fernando, Isla Martín García, *J. Hurrell et al.* 3882 (LP); Isla Martín García, Barrio Chino, *J. Hurrell et al.* 3473 (LP); Pdo. Tigre, Delta, *A. Tuyuparé, A. Scala* 105 (LP). **Catamarca:** Dep. Capayán, por la Ruta 60, entre San Martín y Telaritos, *A. T. Hunziker* 19334 (CORD); Dep. La Paz, El Barrial, *A. Brizuela* 57 (CTES). **Chaco:** Dep. Cmte. Fernández, EEA Sáenz Peña, 6 mar. 1974, *A. O. Bordón s.n.* (CTES-408699); Dep. Mayor L. J. Fontana, Enrique Urien, *A. P. Rodrigo* 2585 (LP); Villa Ángela, *P. Boffa* 1105 (LP). Dep. 1° de Mayo, Colonia Benítez, *A. G. Schulz* 3860, 14707 (ambos en CTES). **Córdoba:** Dep. Capital, Córdoba, *E. L. Ratera* 1076 (CORD); km 1.5 del camino a Chacra de la Merced, 15 feb. 1978, *C. Reudel s.n.* (CORD); Co. de las Rosas, *C. Costa & I. Budini* 100 (CORD); Dep. Cruz del Eje, *A. T. Hunziker* 1800 (CORD); Dep. Punilla, Sa. Chica, falda O, Lago San Roque, *A. T. Hunziker* 6365 (CORD); Dep. San Javier, *A. T. Hunziker* 11483 (CORD); Dep. Tulumba, entre Lucio V. Mansilla y El Tuscal, *A. T. Hunziker* 11011 (CORD). **Corrientes:** Dep. Capital, camino viejo a Laguna Brava, *B. Benítez* 240 (CTES); Escuela de Agricultura, *A. Schinini* 9629 (CTES); Dep. Empedrado, Ea. La Yela, *T. M. Pedersen* 15408 (LP); Dep. Esquina, *A. P. Rodrigo* 3327 (CTES, LP); Dep. Ituzaingó, *J. Daciuk* (LP); Dep. Mburucuyá, *T. M. Pedersen* 1108 (LP). **Entre Ríos:** Dep. Concordia, Yuquerí (INTA), *A. Burkart & N. Troncoso* 27228 (CTES); Represa de Salto Grande, *N. Troncoso et al.* 3573 (SI); Dep. Gualeguaychú, *A. Burkart et al.* 25729 (CTES); Dep. La Paz, Ea. La Invernada, *A. Burkart & N. M. Bacigalupo* 21182 (CTES). **Formosa:** Dep. Bermejo, Laguna Yema, *N. D. Bayón & C. A. Moreno* 876, 878 (ambos en LPAG); Dep. Formosa, Formosa, ribera del Paraguay, *G. Delucchi* 1940 (LP); Dep. Patiño, Ibarreta, 7 abr. 1972, *A. O. Bordón s.n.* (CTES-410133). **Jujuy:** Dep. Santa Bárbara, entre Vinalito y Palma Sola, *A. L. Cabrera & H. A. Fabris* 22702 (CTES); Dep. Ledesma, Calilegua, *A. L. Cabrera* 27907 (CTES). **La Rioja:** Dep. Arauco, Aimogasta, *A. T. Hunziker* 4981, 4987 (ambos en CORD); Dep. Capital, ciudad de La Rioja, *A. T. Hunziker* 4698 (CORD); Cochangasta, camino al Dique de los Sauces, *A. T. Hunziker* 4694, 5138 (ambos en CORD); Dep. Chamical, Ruta Nac. 79 entre Chamical y Olta, *F. Biurru & E. Pagliari* 2111 (CORD); Dep. Grl. Belgrano, Sa. de los Llanos, Dique de Olta, *A. T. Hunziker & T. E. Di Fulvio* 14444 (CORD); Dep. Grl. Ocampo, Santa Rita de Catuna, *F. Biurru et al.* 750 (CORD); Dep. Gob. Gordillo, Polco, *S. Rosas et al.* 619 (CORD); Dep. Sanagasta, Sanagasta, *A. T. Hunziker* 4742, 4862 (ambos en CORD). **Mendoza:** San Rafael, *H. A. Lagiglia* 1439 (LP). **Misiones:** Dep. Cainguás, Puerto Rico, *J. E. Montes* 4052 (LP); Dep. Candelaria, Santa Ana, *E. Schwindt* 75 (CTES); s. loc., *J. E. Montes* 2229 (LP); Yabebiry, *J. E. Montes* 689 (LP); Dep. Eldorado, Eldorado, Salto Elena, *A. Fernández et al.* 29 (CTES); Dep. Iguazú, *Rodrigo* 3674 (LP); Puerto Istueta, *J. E. Montes* 10223 (LP); Puerto Istueta, Km. 14, *J. E. Montes* 9298 (CTES); Dep. Lib.

Grl. San Martín, Ruiz de Montoya, aldea Takuapi, *H. A. Keller* 2991 (CTES). **Salta:** Dep. La Viña, Qda. de las Conchas, Anfiteatro, *A. L. Cabrera et al.* 23756 (LP); Dep. Rivadavia, Santa Victoria Este, *G. F. Scarpa* 626, 642 (ambos en CTES). **San Juan:** Dep. Angaco, Sa. de Pie de Palo, subiendo a Mogote Los Corralitos, en la Qda. del Molle, *A. T. Hunziker et al.* 23795 (CORD). **Santiago del Estero:** Dep. Choya, Frías, *A. T. Hunziker* 2520, 2524, 2525 (los tres en CORD); Dep. Grl. Taboada, Los Juríes, *A. Krapovickas* 852 (CORD). **Tucumán:** Dep. Capital, Río Salí, *L. Venturi* 2839 (LP). BRASIL. **Santa Catarina:** Mun. Aguas de Chapecó, *L. B. Smith & R. M. Klein* 14089 (LP). ECUADOR. **Galápagos:** Isla Santa Cruz, a mitad de camino hacia Bella Vista, *L. A. Fournier* 210 (US). PARAGUAY. **Boquerón:** Mcal. Estigarribia, *A. Schinini & R. Palacios* 25557 (CTES); Tte. Ochoa, *A. Schinini & R. Palacios* 25588 (CTES); Ruta Trans Chaco, *A. Schinini & R. Palacios* 25782 (CTES). **Caaguazú:** ca. Cnel. Oviedo, *T. M. Pedersen* 8447 (CTES). **Guairá:** Berja, *J. E. Montes* 16222 (CTES); s. loc., *P. Jørgensen* 3439 (LP). **Misiones:** Santiago, Ea. La Soledad, *T. M. Pedersen* 7654 (CTES). **Pres. Hayes:** Ea. La Perla, *T. M. Pedersen* 14625 (CTES).

ISRAEL. Tel Aviv, Shekhunat Borocho, *A. Eig* 10368 (CTES).

II. 51. *Amaranthus viscidulus* Greene, Pittonia 3(19): 344. 1898. TIPO: Estados Unidos de América. Nuevo México: Lincoln Co., Sa. Blanca Peak, al S de Carrizozo, 7000 ft., 6 ago. 1897, *E. O. Wootton* 300 (holotipo, NDG [código de barras] NDG15529 no visto, imagen!; isotipos, US [cb] US00106266 no visto, imagen!, US [cb] US00106267 no visto, imagen!, GH [cb] GH00037018 no visto, imagen!). Figura 65.

Hierbas anuales algo suculentas; tallos principales erectos, ascendentes o postrados, 0.2–0.3(–1) m, ramificados, fuertes o débiles, con pubescencia glandular densa, a veces volviéndose glabros con la edad, con tonalidades de color rojizo o a veces blancuzco. Hojas con pecíolo de 5–25 mm, viscoso-pubescentes en la cara abaxial, glabrescentes en la adaxial, algo carnosas, lámina oblonga, ovada, rómbico-ovada, obovada o espatulada, no o algo ondulada, 1–4.5 × 0.5–2.5 cm, cuneada en la base, obtusa o apenas emarginada en el ápice, de color verde pálido o amarillento, mucronada. Inflorescencias terminales y axilares, las primeras en una espiga rígida, 2–10 × 1–2 cm, erecta, no ramificada, de color verdoso o rojizo; las segundas en glomérulos axilares; brácteas y bractéolas lanceoladas a subulado-lanceoladas, 5–8 mm, espinescentes, varias veces más largas que los sépalos. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas, con 5 sépalos, 3 o 4(5) estambres. Flores pistiladas, con 5 sépalos oblongos, 1.5–2.5 mm, con la vena media marcada, excurrente, obtusos o subagudos, el interior menor; estigmas 3, alargados, notablemente engrosados en la base. Frutos dehiscentes, 1.3–2.5 mm, iguales o

apenas superando a los sépalos, lisos o rugosos; semillas de color negro, 1–1.2 mm, brillantes.

Distribución y ecología. *Amaranthus viscidulus* es una especie de los Estados Unidos de América (Nuevo México) que crece en planicies inclinadas y secas y en hábitats disturbados, entre los 1500 m y los 2500 m (Mosyakin & Robertson, 2003).

Discusión. *Amaranthus viscidulus* se asemeja a *A. torreyi* y *A. undulatus* por presentar inflorescencias terminales espiciformes, no ramificadas. Sin embargo, *A. viscidulus* se distingue por el hecho de que sus flores pistiladas poseen brácteas y bractéolas varias veces más largas que los sépalos, mientras que en *A. torreyi* y *A. undulatus* las brácteas y bractéolas son a los sumo algo mayores que los sépalos. Por otra parte, *A. viscidulus* se particulariza por presentar hojas de consistencia carnosa con pubescencia viscosa en su cara abaxial. Por sus brácteas y bractéolas largas y rígidas, podría confundirse con *A. powellii*, pero esta última carece de pubescencia glandulosa.

II. 52. *Amaranthus vulgatissimus* Speg., Anales Soc. Ci. Argent. 53 (1): 281. 1902. TIPO: Argentina. Buenos Aires: Carmen de Patagones, 6 dic. 1911, *C. Berg* 166 (neotipo, aquí designado, LP-033733!). Figura 66.

Amaranthus ataco Thell., Repert. Spec. Nov. Regni Veg. 16: 23–24. 1919, as “*Amarantus ataco*”. TIPO: Argentina. Jujuy: “Morena in cultis, loco humido”, 3500 m, 26 feb. 1901, *R. E. Fries* 876 (lectotipo, aquí designado, S-07-12523!; isoelectotipos, S-07-12522!, US [código de barras] US00106232 no visto, imagen!).

Hierba perenne; tallos principales decumbentes, 10–40 cm, glabros, ramificados desde la base. Hojas con pecíolo de 0.3–2.5, glabras, lámina lanceolada a ovada, ondulada, 1–3.5 × 0.5–1.5 cm, cuneada en la base, aguda a obtusa, mucronada. Inflorescencias axilares, en glomérulos, los cuales al aproximarse en el ápice forman panículas de 2(–4) cm, sin hojas en la porción distal; brácteas y bractéolas ovadas, 0.7–1.5 mm, ápice agudo, mucronado. Flores de ambos sexos en la misma inflorescencia. Flores estaminadas con 5 sépalos oblongos a elípticos, 1.3–1.5 mm, subobtusos, mucronados, 5 estambres. Flores pistiladas con 5 sépalos oblongo-obovados a oblongo-espátulados, 1.5–2.2 mm, base 0.3–0.5 mm de ancho, levemente adelgazados hacia la base, obtusos, inflexos y adpresos al fruto, mucronados; estigmas tres, 0.3 mm. Frutos indehiscentes, rugosos, igualando en longitud a los sépalos o algo más breves; semillas de color negro, 1–1.3 mm, punteadas.

Distribución y ecología. *Amaranthus vulgatissimus* constituye un endemismo de la región central y occidental de Argentina. Esta especie crece en áreas secas, abiertas, con vegetación achaparrada, sobre suelos gravosos con escasa cobertura, a veces en cursos de agua secos (*Pedersen 15221*, CTES, SI) entre el nivel del mar y los 3000 m (Pedersen, 1994). Florece entre los meses de octubre y abril.

Nombre vulgar. Ataco silvestre (de la Peña & Pensiero, 2004).

Discusión. Los frutos lisos e indehiscentes de *Amaranthus vulgatissimus* recuerdan por un lado a los de *A. deflexus*, pero esta última especie tiene dos sépalos en sus flores pistiladas, mucho más cortos que el fruto, y no cinco sépalos de la misma longitud como en los frutos de *A. vulgatissimus*. Se asemeja también a *A. lombardoi*, aunque esta especie tiene tres o cuatro sépalos en sus flores pistiladas, los que son lineares con una giba basal, mientras que *A. vulgatissimus* tiene cinco sépalos no oblongos ni gibosos. Con respecto a las especies con frutos indehiscentes y cinco sépalos en sus flores pistiladas (como *A. crispus*, *A. cuspidifolius*, *A. cochleitepalus*, *A. persimilis* o *A. standleyanus*), todas ellas tienen sépalos distintamente espátulados con la base estrecha de menos de 0.3 mm de ancho, mientras que *A. vulgatissimus* tiene sépalos oblongos que superan ese ancho en la base (0.3–0.5 mm de ancho).

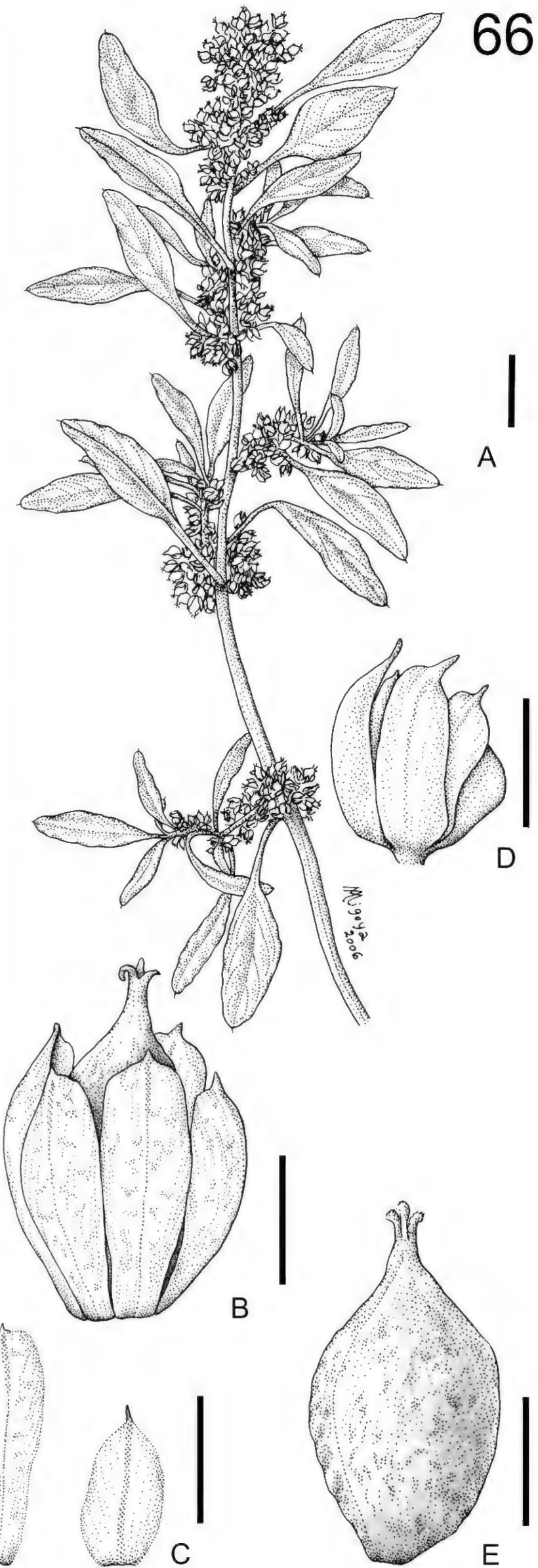
Cuando C. Spegazzini (1902: 281) cita el material en la descripción original de *Amaranthus vulgatissimus* dice: Argentina. Río Negro: “Non rarus in cultis secus Rio Negro prope Carmen de Patagones, Febr. 1898, *C. L. Spegazzini s.n.*”. Covas (1941: 341) cita como probable tipo a “*C. Spegazzini 12068* (L.P. Sp.)”. Este ejemplar no se halla en el herbario LP por lo que se designa como neotipo a un material de la misma localidad del ejemplar que eligiera el autor de la especie, pero coleccionado por Berg.

Por otro lado, al describir *Amaranthus ataco*, Thellung (1919b: 23) menciona tres sintipos en la descripción original, ellos son: *R. E. Fries* 876, *F. Philippi s.n.* y *Osten s.n.* (Herb. Hassler 13451). Del primero existen dos ejemplares en el herbario S (S-07-12522 y S-07-12523) y un tercero en el herbario US (US [código de barras] US00106232). He estudiado las flores femeninas de los dos ejemplares depositados en S. Concluyo que tal como sugiriera Pedersen (1999), esta especie es un sinónimo de *A. vulgatissimus*. Además los ejemplares de Fries se asemejan a *A. vulgatissimus* por sus hojas pequeñas, no mayores a 3.5 cm, y sus inflorescencias principalmente axilares. Por otro lado, del ejemplar de Osten he recibido una imagen del herbario G que

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se corresponde con *A. ataco*. Finalmente, en el herbario SGO he estudiado un ejemplar que muestra dos etiquetas de F. Philippi: la inferior coincide con el protólogo de Thellung (1919b: 23) pues cita como localidad de colección a “Antofagasta” y la fecha “Ene. 1885”; además dice “*Euxolus caudatus*, Ataco”. Por el contrario, en la etiqueta superior figura como localidad “Santiago” y la fecha “Abr. 1882”, como así también el nombre “*Euxolus caudatus* Moq”. Este ejemplar de SGO no se corresponde con la especie bajo consideración, pues sus hojas son mucho mayores, de hasta 12 cm y las inflorescencias apicales son caudadas de hasta 12 cm (siendo que en *A. vulgarissimus* pueden darse inflorescencias terminales pero sin exceder los 2 cm). El ejemplar montado sobre esta cartulina parece pertenecer a *A. caudatus* L., no correspondiéndose con la descripción de *A. ataco*. Teniendo en cuenta todo lo dicho, de los dos ejemplares *Fries* 876 depositados en S, se designa como lectotipo de la especie al ejemplar S-07-12523 dado que el mismo cuenta con una planta completa, con abundantes hojas e inflorescencias, que se corresponden en un todo con la diagnosis original.

Ejemplares examinados. ARGENTINA. **Buenos Aires:** Pdo. Lobería, Lobería, *A. Scala s.n.* (LP-24116). **Chubut:** Dep. Viedma, Puerto Madryn, *G. Bonarelli* 32173 (BA). **Córdoba:** Dep. Calamuchita, Villa Gral. Belgrano, *A. Krapovickas & C. L. Cristóbal* 14652 (CTES); Dep. Colón, Sa. Chica, falda E, en la Qda. de los Hornillos, *A. T. Hunziker* 6896 (CORD); Dep. Cruz del Eje, Sa. Grande, Dos Ríos, entre Río Guasta y Río Chaves, *A. T. Hunziker* 8834 (CORD); Dep. Ischilín, ca. Deán Funes, km 817 de la Ruta 60, *A. T. Hunziker et al.* 22002 (CORD); Dep. Ischilín/Punilla, Sa. Copacabana, falda O, en Monteros, *A. T. Hunziker* 9728 (CORD); Dep. Ischilín/Tulumba, *A. T. Hunziker* 9802 (CORD); Dep. Minas, Sa. Guasapampa, falda O, ca. de Ojo de Agua, *A. T. Hunziker* 9164 (CORD); Dep. Pocho, Sa. de Pocho, falda O, Ruta 20, ca. de los túneles, *A. T. Hunziker et al.* 14023 (CORD); Sa. de Pocho, falda N del Co. Yerba Buena, *A. T. Hunziker* 9817 (CORD); Sa. de Pocho, entre Las Palmas y la Mundana, *A. T. Hunziker* 9786 (CORD); Sa. Grande, falda O, cuesta de las Chacras, alr. de Tala Cañada, *A. T. Hunziker* 9886 (CORD); Pampa de Pocho, frente al Co. Puntudo, en el camino de Taninga a La Rioja, *A. T. Hunziker* 8861 (CORD); cumbre de Gaspar, falda O, cuesta de Las Chacras, entre A. Murúa y A. Albarracín (Ruta 20), *A. T. Hunziker* 8849 (CORD); Dep. Punilla, Sa. Chica, La Falda, 4 abr. 1918, in campis vaseosis, *Osten s.n.*; Herb. Hassler n° 13451 (sintipo, *Amaranthus ataco*, G no visto, imagen!), Los Cocos, *A. V. de*

la Sota 3254 (CORD); Sa. Grande, falda E, entre Tanti y El Durazno, *A. T. Hunziker* 10537 (CORD); Sa. Chica: falda O, Cruz Chica, entre Los Cocos y La Cumbre, *A. T. Hunziker* 8958 (CORD); Sa. Chica: falda O, La Cumbre, Co. de la Cruz, *A. T. Hunziker* 8916 (CORD); Sa. Chica: falda O, Co. Uritorco, 27 ene. 1922, *A. Castellanos s.n.* (CORD); Sa. Grande, falda E, Ea. San Bernardo, *A. T. Hunziker* 12019, 12032 (ambos en CORD); en la falda de qda. sobre orilla NO del Lago San Roque, *A. T. Hunziker* 6356 (CORD); Sa. Chica, Co. Uritorco, falda O, *A. T. Hunziker & A. E. Cocucci* 17863 (CORD); Villa del Lago, *A. V. de la Sota* 3570 (CTES); Dep. San Alberto, Sa. Grande, Pampa de Achala, ca. La Posta, *A. T. Hunziker* 8759, 11689 (ambos en CORD); s. loc., 20 dic. 1952, *M. M. Job s.n.* (CTES); Dep. San Javier, Sa. Grande, falda O, Cuesta de las Cabras, falda O del Co. Champaquí, ca. de la Qda. del Tigre, *A. T. Hunziker* 9524 (CORD); Dep. Totoral, Sa. Chica falda E, Ea. San Miguel, *A. T. Hunziker* 4883 (CORD); Dep. Tulumba, Co. Sauce Punco, *A. R. Cuezco* 754 (CORD). **Jujuy:** Dep. Humahuaca, *L. Herrera* 419 (CTES). **La Rioja:** Dep. Famatina, Sa. de Famatina, Guanchín, 23 ene. 1928, *A. Castellanos s.n.* (BA); La Aguadita, *F. O. Zuloaga* 24643 (CTES). Dep. Grl. Belgrano, Sa. de los Llanos, Dique de Olta, *A. T. Hunziker* 14463 (CORD). Dep. Gral. Lavalle, Cuesta de Miranda, *A. L. Cabrera et al.* 24580 (CTES). **Mendoza:** Dep. Capital, Parque, 24 ene. 1901, *C. L. Spegazzini s.n.* (BAB); Dep. Luján, Cacheuta, *R. Palacios et al.* 2783 (CTES); Dep. Las Heras, entre Potrerillos y Uspallata, *F. A. Roig* 4297, 10202 (ambos en CTES); Dep. Potrerillos, A. Próximo, Ea. El Sosneado, *H. A. Lagiglia* 614 (LP); s. loc., *L. Garola* 117 (BAB). **Salta:** Dep. San Carlos, Amblayo, ene. 1897, *C. L. Spegazzini s.n.* (LP). **San Juan:** Dep. Angaco, Sa. Pie de Palo, camino al Mogote Los Corralitos, en la Qda. del Molle, *A. T. Hunziker et al.* 23807 p.p. (CORD); Sa. de Pie de Palo, camino a Mogote de los Corralitos, *R. Kiesling* 3097 (CTES); Dep. Iglesia, camino entre Pismanta y Paso de Agua Negra, *A. T. Hunziker & R. Subils* 24570 (CORD); Qda. Agua Negra, *A. L. Cabrera* 24371 (LP); Dep. Calingasta, Qda. de las Burras, Vega del Mal Paso, *R. Kiesling et al.* 7444 (CTES, SI); Potrero de las Burras, *R. Kiesling et al.* 7395 (SI); Dep. Iglesia, Arrequeintín, *T. M. Pedersen* 15270 (SI); Dep. Sarmiento, Río Bachongo, *R. Guaglianone et al.* 1474 (CTES); Dep. Ullún, entre Talacasto y Alto del Colorado, *R. Kiesling & A. Sáenz* 4240 (SI); Qda. de las Burras, *T. M. Pedersen* 15221 (CTES, SI). **San Luis:** Dep. La Capital, Potrero de los Funes, *A. Castellanos* 25/673 (CORD); Co. Varela, Qda. La Chilca, *D. L. Anderson* 1918 (CORD); Co. de la Aguada, *D. L. Anderson* 3461 (CORD); Potrero de los Funes, 27 feb. 1925, *Castellanos s.n.* (BA); Dep. Grl. Pedernera, Co. El Morro, Ea. La Morena, *A. T. Hunziker* 12648 (CORD); Dep. Grl. San Martín, Sa. de San Luis, entre Concarán y San Martín, *A. T. Hunziker & A. E. Cocucci* 14573 (CORD); sin dep. det., Sa. de San Luis, Piedra del Agua, 22 dic. 1929, *A. Castellanos s.n.* (BA); sin dep. det., Pancanta, 22 feb. 1925, *A. Castellanos s.n.* (BA). **Tucumán:** Dep. Tafí, Infiernillo, 5 km al O de la cima, *T. M. Pedersen* 15356 (CTES).

Figura 65. *Amaranthus viscidulus* Greene. —A. Hábito fértil. A, ilustrado de Wootton 300 (NY). La barra de escala para A = 1 cm.

Figura 66. *Amaranthus vulgarissimus* Speg. —A. Hábito fértil. —B. Flor pistilada. —C. Sépalos y bráctea de la flor pistilada. —D. Flor estaminada. —E. Fruto. A–E, ilustrado de Kiesling 7444 (SI). La barra de escala para A = 1 cm; para B–E = 1 mm.

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surge de la Lista de Especies Aceptadas que se brinda a continuación. I. *Amaranthus* L. subg. *Amaranthus*; II. *Amaranthus* subg. *Albersia* (Kunth) Gren. & Godr.

LISTA DE ESPECIES ACEPTADAS

- II. 1. *A. acutilobus* Uline & W. L. Bray
- II. 2. *A. albus* L.
- II. 3. *A. anderssonii* J. T. Howell
- I. 1. *A. asplundii* Thell.: I. 1a. *A. asplundii* subsp. *asplundii*; I. 1b. *A. asplundii* subsp. *australis* (Hunz.) N. Bayón
- II. 4. *A. blitoides* S. Watson
- II. 5. *A. blitum* L.: II. 5a. *A. blitum* subsp. *blitum*; II. 5b. *A. blitum* subsp. *emarginatus* (Uline & W. L. Bray) Carretero, Muñoz Garmendia & Pedrol; II. 5c. *A. blitum* subsp. *oleraceus* (L.) Costea; II. 5d. *A. blitum* subsp. *pseudogracilis* (Thell.) N. Bayón
- II. 6. *A. brownii* Christoph. & Caum
- II. 7. *A. californicus* (Moq.) S. Watson
- II. 8. *A. capensis* Thell.: II. 8a. *A. capensis* subsp. *capensis*; II. 8b. *A. capensis* subsp. *uncinatus* (Thell.) Brenan
- I. 2. *A. cardenasianus* Hunz.
- I. 3. *A. caudatus* L.
- II. 9. *A. centralis* J. Palmer & Mowatt
- II. 10. *A. clementii* Domin
- II. 11. *A. cochleitepalus* Domin
- II. 12. *A. crassipes* Schldtl.: II. 12a. *A. crassipes* subsp. *crassipes*; II. 12b. *A. crassipes* subsp. *warnockii* (I. M. Johnst.) N. Bayón
- II. 13. *A. crispus* (Lesp. & Thévenau) J. M. Coult. & S. Watson
- I. 4. *A. cruentus* L.
- II. 14. *A. cuspidifolius* Domin
- II. 15. *A. deflexus* L.
- II. 16. *A. dinteri* Schinz: II. 16a. *A. dinteri* subsp. *brevipetiolatus* Brenan. II. 16b. *A. dinteri* subsp. *dinteri*
- I. 5. *A. dubius* Mart.
- I. 6. *A. fimbriatus* (Torr.) S. Watson
- II. 17. *A. furcatus* J. T. Howell
- II. 18. *A. graecizans* L.: II. 18a. *A. graecizans* subsp. *aschersonianus* (Thell.) Costea, D. M. Brenner & Tardif; II. 18b. *A. graecizans* subsp. *graecizans*; II. 18c. *A. graecizans* subsp. *sylvestris* (Vill.) Brenan; II. 18d. *A. graecizans* subsp. *thellungianus* (Vassilcz.) Gusev
- II. 19. *A. grandiflorus* (J. M. Black) J. M. Black
- II. 20. *A. hunzikeri* N. Bayón
- I. 7. *A. hybridus* L.: I. 7a. *A. hybridus* subsp. *hybridus*; I. 7b. *A. hybridus* subsp. *quitensis* (Kunth) Costea & Carretero
- I. 8. *A. hypochondriacus* L.
- II. 21. *A. induratus* J. Palmer & Mowatt
- II. 22. *A. interruptus* R. Br.
- II. 23. *A. kloosianus* Hunz.

APÉNDICE 1

Índice de colecciones. Las colecciones están ordenadas alfabéticamente por colector y por el número de colección seguido por el número de la especie entre paréntesis, el que

II. 24. *A. lombardoi* Hunz.
II. 25. *A. looseri* Suess.
II. 26. *A. macrocarpus* Benth.: II. 26a. *A. macrocarpus* subsp. *macrocarpus*; II. 26b. *A. macrocarpus* subsp. *pallidus* (Benth.) N. Bayón
II. 27. *A. minimus* Standl.
II. 28. *A. mitchellii* Benth.
II. 29. *A. muricatus* (Moq.) Hieron.
II. 30. *A. obcordatus* (A. Gray) Standl.
II. 31. *A. pedersenianus* N. Bayón & C. Peláez
II. 32. *A. persimilis* Hunz.
II. 33. *A. peruvianus* (Schauer) Standl.
II. 34. *A. polygonoides* L.
I. 9. *A. powellii* S. Watson
II. 35. *A. praetermissus* Brenan
II. 36. *A. pumilus* Raf.
I. 10. *A. retroflexus* L.
II. 37. *A. rhombeus* R. Br.
II. 38. *A. rosengurtii* Hunz.
I. 11. *A. scariosus* Benth.
II. 39. *A. schinzianus* Thell.
II. 40. *A. sclerantoides* (Andersson) Andersson
II. 41. *A. scleropoides* Uline & W. L. Bray
I. 12. *A. spinosus* L.
II. 42. *A. squamulatus* (Andersson) B. L. Rob.
II. 43. *A. standleyanus* Covas
II. 44. *A. tamaulipensis* Henrickson
II. 45. *A. thunbergii* Moq.
II. 46. *A. torreyi* (A. Gray) S. Watson
II. 47. *A. tricolor* L.
II. 48. *A. undulatus* R. Br.
II. 49. *A. urceolatus* Benth.
II. 50. *A. viridis* L.
II. 51. *A. viscidulus* Greene
II. 52. *A. vulgatissimus* Speg.
I. 13. *A. wrightii* S. Watson

Abbiatti, B. 4447 (II. 13). Abbiatti, B. & L. Claps 1018 (I. 7a), 18 (I. 7b), 931 (I. 7b), 230 (I. 12), 304 (II. 43). Aellen, P. 1960 (II. 5a), 152 (II. 18c), s.n. (I. 7a). Aellen, P. & W. Baumgartner 25 (I. 12). Agnér, H. s.n. (II. 5a). Aguirre, E. 352 (II. 43). Ahles, H. E. 89043 (II. 2), 81287 (I. 7a). Ahumada, O. & A. Castellón 4910 (I. 12), 4745 (II. 43). Alboff s.n. (I. 7b). Anderson, D. L. 1076 (II. 2), 3018 (II. 2), 3097 (II. 23), 2463 (II. 23), 3802 (II. 23), 3018 (II. 43), 3097 p.p. (II. 43), 1918 (II. 52), 3461 (II. 52). Anderson, D. L. & J. E. Alliney 3046 (II. 2). Andersson, N. J. s.n. (II. 40) [tipo, *Amaranthus sclerantoides*]. Arbo, M. M. & A. Schinini 2424 (II. 38). Arenas, P. 209, 409 (I. 7b), 2381 (I. 7b), 1110 (II. 29), 1901 (II. 33). Arenas, P. & A. Dell'Arciprete 1746 (I. 1a). Argañaráz, J. L. 22 (I. 7b). Ariza Espinar, L. 602 (II. 29). Arsène, G. 6121 (II. 1), 7104 (II. 1), s.n. (I. 8). Asplund, E. 2988 (I. 1a) [tipo, *A. buchtienianus*], 3838 (I. 1a) [tipo, *A. buchtienianus*], 4071 (I. 1a) [tipo, *A. asplundii*], 722 (II. 5a), 5027 (II. 49), 5140 (II. 49). Augustin, F. 4094 (I. 4).
Badini, L. 24014 (I. 12). Báez, J. R. 101 (II. 13). Baker, C. F. 1855 (II. 7). Barboza et al. 1453 (II. 31) [tipo, *Amaranthus pedersenianus*], 1455 (II. 31) [tipo, *A. pedersenianus*]. Bayard

Long 61638 (I. 10). Bayón, N. D. 626 (II. 5d), 1332 (II. 5d), 608 (I. 4), 627 (I. 4), 1354 (I. 4), 337 (II. 15), 625a (II. 15), 1344 (II. 15), 629 (I. 7a), 1097 (I. 7a), 1540 (I. 7a), 605 (I. 7b), 615 (I. 7b), 633 (I. 7b), 642 (I. 7b), 1090 (I. 8), 625b (II. 29), 1353 (II. 29), 1355 (II. 29), 603 (II. 50), 1093 (II. 50), 1329 (II. 50). Bayón, N. D. & C. A. Moreno 835 (I. 7b), 716 (II. 29), 880 (II. 29), 717 (II. 43), 785 (II. 43), 876 (II. 50), 878 (II. 50). Bayón, N. D. & J. Vera Bahima 1456 (II. 20), 1457 (II. 20), 1462 (II. 20), 1463 (II. 20), 1485 (II. 20). Bang M. 97 (I. 7a). Bartlett, N. H. 19933 (II. 13). Bates, R. J. 46838 (II. 28). Beck, G. 7988 (I. 2), 1396 (I. 7a), 2713 (I. 12). Belshaw, C. M. 2674 (II. 7). Benítez, B. 240 (II. 50). Benítez, B. et al. 132 (II. 5b). Bentley, P. S. 150 (II. 40). Berg, C. 135 (I. 7b), s.n. (I. 7b), s.n. (II. 15), 166 (II. 52) [tipo, *A. vulgatissimus*]. Berlandier, J. L. 2276 (I. 7a). Bermejós, J. 39771 (II. 47). Bessey, C. E. s.n. (II. 4) [tipo, *A. blitoides*]. Birabén, M. 66 (I. 7b), 5343 (I. 7b), 3021 (II. 43). Biurrun, F. & C. Agüero 1721 (II. 43). Biurrun, F. & L. Blanco 7480 (II. 23), 7370 (II. 43), 7382 (II. 43), 7472 (II. 43). Biurrun, F. & E. Biurrun 6765 (I. 7b), 6766 (II. 43). Biurrun, F. & E. Pagliari 2211 (II. 13), 58 (II. 43), 2111 (II. 50). Biurrun, F. et al. 7148 (I. 7b), 3559 (II. 23), 7047 (II. 29), 7203 (II. 29), 4836 (II. 32), 7026 (II. 43), 750 (II. 50). Blakly, R. E. H3407 (I. 8). Blanchet, G. 17 (I. 10). Bodenbender 8998 (II. 23) [tipo, *A. kloosianus*]. Boelcke, O. 1472 (II. 5b), 4224 (I. 7b). Boelcke, O. & J. Gimara 6 (I. 7a). Boettcher, F. L. J. s.n. (II. 2). Boffa, P. 1103 (I. 7b), 1105 (II. 50). Bona Nascimento, M. S. 25 (I. 12). Bonarelli, G. 32173 p.p. (II. 52). Bordas, E. 3962 (I. 7b). Bordón s.n. (I. 7b), s.n. (II. 50). Bouchon s.n. (I. 7a) [tipo, *A. bouchonii*]. Boyd, S. 6415 (II. 4), 6436 (II. 4). Braun, A. s.n. (II. 1) [tipo, *A. acutilobus*]. Brenan, J. P. M. 14089 (II. 8a), 14080 (II. 16b), 14172 (II. 35). Brizuela, A. 954 (II. 23), 954 dupl. p.p. (II. 23), 954 dupl. p.p. (II. 43), 970 (I. 7b), 1012 (I. 7b), 1111 (I. 7b), 1150 (I. 7b), s.n. (I. 7b), 954 dupl. p.p. (II. 23), 954 (II. 23), 1478 (II. 29). Brizuela, J. 1615 (II. 15), 57 (II. 50). Bruch-Carette 24 (II. 43), 87 (II. 43). Bruno, C. A. 171 (I. 7b). Buchinger s.n. (II. 29). Buchtien, O. s.n. (I. 7b). Bueno, O. 1413 (I. 7b). Bühner, H. s.n. (II. 2), s.n. (I. 10). Burkart, A. s.n. (II. 2), 3828 (II. 2), 18232 (II. 5b), 29860 (II. 5b), 17809 (I. 3), 10849 (II. 13), 10878 (II. 13), 15577 (I. 4), 21722 (I. 7b), 29314 (I. 7b), 30827 (II. 29), 25925 (II. 38). Burkart, A. & N. Troncoso 27228 (II. 50). Burkart, A. & N. M. Bacigalupo 21182 (II. 50). Burkart, A. et al. 25726 (I. 7b), 23329 (II. 29), 23332 (II. 29), 25723 (II. 29), 25727 (II. 38), 25925 (II. 38), 25729 (II. 50). Burkitt, G. s.n. (II. 28).
Caballero Marmori, G. 1447 (II. 29). Cabezas, V. 56 (II. 33). Cabrera, A. L. 12153 (I. 1a), 7940 (II. 5b), 10214 (II. 5b), 14724 (II. 5b), 7570 (II. 13), 1739 (II. 15), 5153 (II. 15), 5707 (II. 15), 10058 (II. 15), 10157 (II. 15), 22451 (II. 20), 2790 (I. 7b), 4123 (I. 7b), 5155 (I. 7b), 6312 (I. 7b), 7459 (I. 7b), 10215 (I. 7b), 1199 (I. 7b), 1943 (I. 7b), 2647 (II. 29), 5201 (II. 29), 8697 (II. 31) [tipo, *Amaranthus pedersenianus*], 8971 (II. 31) [tipo, *A. pedersenianus*], 4179 (I. 12), 10872 (I. 12), 10935 (I. 12), 1083 (II. 43), 7503 (II. 43), 23734 (II. 43), 5227 (II. 50), 10059 (II. 50), 27907 (II. 50), 24371 (II. 52). Cabrera, A. L. & H. A. Fabris 19912 (I. 7b), 22679 (I. 7b), 22702 (II. 50). Cabrera, A. L. & R. Kiesling 25199 (I. 7b). Cabrera, A. L. & J. M. Marchionni 12732 (I. 7b), 12760 (I. 7b). Cabrera, A. L. & E. M. Zardini 23869 (I. 7b). Cabrera, A. L. et al. 16897 (I. 1a), 15036 (II. 20), 22451 (II. 20), 32442 (II. 20), 13372 (I. 7a), 291 (I. 7b), 14601 (I. 7b), 15158 (I. 7b), 21753 (I. 7b), 21755 (I. 7b), 26031 (I. 7b), 31523 (I. 7b), 26341 (II. 29), 27386 (II. 31) [tipo, *A. pedersenianus*], 234 (I. 12), 289 (I. 12), 4179 (I. 12), 31416 (I. 12), 34408 (I. 12),

13786 (II. 43), 14246 (II. 43), 14404 (II. 43), 14622 (II. 43), 23256 (II. 43), 23354 (II. 43), 23756 (II. 50), 24580 (II. 52). Camp, W. H. E-2443 (I. 7b), E-2551 (I. 7b), E-2966 (I. 12). Campbell, J. & J. Pickard s.n. (II. 28). Cantino, P. 489 (II. 43), 727 (II. 43), 765 (II. 43). Capparelli, A. 54 (II. 43). Cárdenas, M. 4137 (I. 2) [tipo, *A. cardenasianus*], 3626 (I. 3), 3627 (I. 3). Carette, E. s.n. (II. 15), s.n. (II. 43). Carrick, P. 9 (II. 5b). Carette, E. s.n. (II. 13), s.n. (II. 29). Castellanos, A. s.n. (II. 13), 47715 (II. 13), s.n. (II. 15), s.n. (II. 20) [tipo, *A. hunzikeri*], s.n. (II. 29), 25/677 (II. 43), s.n. (II. 52), 25/673 (II. 52). Castrejón, C. 25 (I. 12). Castillo, A. 2507 (I. 5), 2552 (I. 5). Castillo, A. & A. De Franca 2635 (I. 12). Castellón 58 (II. 15). Caum, E. L. 73 (II. 6) [tipo, *A. brownii*]. Chase, V. H. 10780 (I. 10). Chippendale, G. 1881 (II. 11), 4668 (II. 14). Chinnock, R. J. 3529 (II. 28). Chrtek 303 (II. 13). Cîrtu, D. & M. Cîrtu 920 (II. 2). Cîrtu, D. & I. Teodorescu 918 (I. 10), 919 (I. 10). Clement, E. s.n. (II. 48). Compton, R. H. 10399 (II. 16b), 23989 (II. 16b), 23999 (II. 35). Cooray, R. G. 70032519R (II. 18d). Copley, B. 1311 (I. 7a). Cory, V. L. 44562 (II. 41). Costa, C. & I. Budini 100 (II. 50). Covas, G. 1049 (II. 13), 1131 (I. 7b), 1216 (I. 7b), 1084 (II. 29), 1121 (II. 43), 1136 (II. 43), 1141 (II. 43), 1148 (II. 43), 1181 (II. 43), 1186 (II. 43). Coveny, R. & K. Ingram 10053 (II. 26a). Coveny, R. K. et al. 12506 (II. 26b). Cowie, I. D. 5526 (II. 48). Cranfield, R. J. 6532 (II. 48). Crespo, S. 66 (I. 7b). Crespo, S. & P. Calieres s.n. (II. 13). Cuezso, A. R. 1745 (II. 29), 754 (II. 52). Curtiss 559 (II. 12a).

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Nee, M. J. 32823 (II. 1), 33988 (I. 7b). Nee, M. & J. Soule 33048 (II. 1). Nel, P. & C. Boucher 34 (II. 45). Nicora, E. G. 428 (I. 7b), 4306 (II. 29). Nicora, E. G. et al. 8354 (II. 32). Norris-Roger, A. J. 664 (II. 35). Novara, L. J. 2615 (I. 7b), 3403 (I. 7b), 8789 (I. 12), 3413 (II. 43). Núñez, O. 5 (I. 7b).

O'Donell, C. A. 1626 (II. 4), 1723 (II. 4), s.n. (II. 15), 84 (I. 12), 2642 (II. 43). Okada, K. 3043.1 (I. 1a), 3043.2 (I. 7a). Oliver & Steenkamp 6264 (II. 39). Olney, S. T. s.n. (II. 36). Orcutt, C. R. 1015 (II. 7). Örtendahl, I. 367 (II. 39).

Painter, R. H. 384 (II. 41). Palacios, R. et al. 1738 (II. 32), 2783 (II. 52). Palmer, E. 456 (II. 7) [tipo, *Amaranthus albomarginatus*], 154 (I. 6), 515 (I. 6), 694 (I. 8), 695 (I. 8), 543 (II. 34), 759 (I. 9), 142 (I. 11), 1130 (II. 41), 197 (II. 46) [tipo, *A. chihuahuensis*]. Panella s.n. (II. 15), s.n. (II. 29). Parish, S. B. & W. F. Parish 1143 (II. 7). Parker, C. F. s.n. (II. 36). Parker, R. N. 3480 (II. 45), 4559 (II. 45). Parodi, L. R. 8084 (I. 5), 8536 (I. 5). Pastore, A. 335 (II. 15), 337 (I. 7b). Patridge, W. s.n. (II. 15). Pavetti, C. & T. Rojas 10439 (I. 7b). Pedersen, T. M. 14980 (II. 2), 14925 (II. 4), 14954 (II. 4), s.n. (II. 5a), 7944 (II. 5a), 1097 (II. 5b), 8666 (II. 5b), 10849 (II. 5b), 13326 (II. 13), s.n. (II. 15), 8149 (II. 15), 8255 (II. 15), 10289 (II. 15), 23 (I. 5), 9789 (I. 7a), 14108 (I. 7a), s.n. (I. 7b), 1139 (I. 7b), 14777 (I. 7b), 14923 (I. 7b), 14924 (I. 7b), 15359 (I. 7b), 15909 (I. 7b), 16141 (I. 7b), 1312 (II. 29), 4010 (II. 29), 6454 (II. 29), 14552 (II. 29), 14622 (II. 29), 15196 (II. 32), 15314 (II. 32), 7936 (I. 10), s.n. (II. 38), 16203 (II. 38), 5424 (I. 12), 10756 (I. 12), 13708 (I. 12), 11755 (II. 43), 11770 (II. 43), 14537 (II. 43), 15218 (II. 43), 15300 (II. 43), 1108 (II. 50), 7654 (II. 50), 8447 (II. 50), 14625 (II. 50), 15408 (II. 50), 15221 (II. 52), 15270 (II. 52), 15356 (II. 52). Pedersen, T. M. et al. 24 (II. 2). Peirano s.n. (II. 43). Pensiero, J. & D. Marino 4338 (II. 43). Pergolani, J. s.n. (II. 15). Perrone, V. R. s.n. (I. 12). Peteten, C. A. & A. Molina 1033 (II. 29), 1198 (II. 29). Philippi s.n. (I. 3). Piccinini, B. & A. Leguizamón 2064 (II. 13). Piccinini, B. & C. A. Petetin 3281 (II. 43). Pierotti 99799 (I. 7b). Plowman, T. 8811 (I. 12). Pólgar, S. 639 (II. 2), 739e (II. 2), 2702 (II. 2), 2834 (II. 13), 2453b (I. 9), 2453c (I. 9), 1754 (I. 10), 2708b (I. 10). Popov & Vvedensky 423 (II. 18c). Pott, A. et al. 2275 (II. 5b). Pott, V. J. 167 (I. 12). Powell s.n. (I. 8) [tipo, *A. leucocarpus*]. Pringle, C. G. 795 (II. 46) [tipo, *A. pringlei*]. Probst, R. 2833 (II. 8b).

Quarín, C. 652 (I. 7b).

Rabelo, B. V. et al. 3298 (I. 12). Rafaelli 22 (II. 29). Ragonese, A. 2056 (II. 29). Rahn, K. 286 (I. 7b). Ramírez, N. 2574 (II. 12a). Ramos, J. E. 790 (I. 12). Ratera, E. L. 1076 (II. 50). Reca, A. R. & D. E. Ramadori 17 (II. 20) [tipo, *Amaranthus hunzikeri*]. Rehmann, A. 2983 (II. 39) [tipo, *A. schinzianus*]. Reudel s.n. (II. 50). Rexach, J. s.n. (II. 43).

Ringuelet, E. J. 325 p.p. (II, 15), 324 (I, 7b), 325 p.p. (I, 7b). Rocha, R. 3689 (I, 12). Rodrigo, A. P. 975 (II, 5b), 3425 (II, 15), 3115 (I, 7b), 3527 (I, 7b), 2187 p.p. (II, 43), 2585 (II, 50), 3327 (II, 50), 3674 (II, 50). Rodríguez, V. 478 (II, 15), 16780 (II, 33). Roig, F. A. 7356 (I, 3), 5179 (II, 13), 8884 (II, 13), 7823 (II, 43), 4297 (II, 52), 10202 (II, 52). Rojas, T. 1257 (I, 7b). Rosa-Mato, F. 418 (I, 7b). Rosas, E. et al. 619 (II, 50). Rosengurtt, B. B-9326 (II, 2), B-3805 (II, 5d), B-6844 (II, 38) [tipo, *A. rosengurtii*], B-7213 (II, 38) [tipo, *A. rosengurtii*], B-6844 (II, 38) [tipo, *A. rosengurtii*]. Rosengurtt, B. et al. PE-198 (II, 38) [tipo, *A. rosengurtii*], PE-1031 (II, 38) [tipo, *A. rosengurtii*], 10324 (II, 38). Roy, F. E. 3969 (II, 2). Rubtsoff, P. 3864 (II, 7), 5240 (II, 7). Ruiz Leal, A. 1216 (I, 7b), 2961 (I, 7b), 8992 (II, 23), 990 (II, 29), 2515 (II, 29). Runyon, R. 2345 (II, 12a), 2350 (II, 34), 5936 (II, 34), 5943 (II, 34), 2169 (II, 41). Rust, H. J. 861 (II, 7). Rusby 804 (II, 4) [tipo, *A. blitoides* var. *densifolius*]. Rutawch, F. T. s.n. (II, 2). Ruthsatz, B. 722 (I, 1b).

Saravia Toledo, C. & M. Day 15255 (I, 7b). Saravia Toledo, C. et al. 13038 (I, 7b), 15255 (I, 7b), 13245 (II, 43). Scala, A. s.n. (II, 13), s.n. (II, 15), 107 (II, 15), s.n. (I, 7b), s.n. (II, 29), 105 (II, 50), s.n. (II, 52). Scappini, E. 1705 (I, 7b). Scarpa, G. F. 477 (II, 43), 605 (II, 43), 626 (II, 50), 642 (II, 50). Schessl, M. 131291-1-2 (I, 12). Scheuermann, R. 2832b (II, 4), s.n. (II, 8b) [tipo, *Amaranthus capensis* subsp. *uncinatus*], s.n. (II, 45). Schickendantz 292 (II, 32) [tipo, *A. persimilis*]. Semper, J. s.n. (II, 23), s.n. (II, 32). Shafer, J. A. 11090 (II, 27) [tipo *A. minimus*]. Schiffmacher 629 (II, 5d). Schinini, A. 31075 (II, 4), 8727 (I, 7b), 31074 (I, 10), 9629 (II, 50). Schinini, A. & R. Palacios 25699 (II, 43), 25745 (II, 43), 25557 (II, 50), 25588 (II, 50), 25782 (II, 50). Schinini, A. & S. M. Pire 24189 (II, 43). Schinini, A. & S. Sánchez García 30576 (II, 29), 30683 (II, 29). Schinini, A. & M. Urbani 35778 (I, 7b). Schinini, A. et al. 19254 (I, 7b). Schreiter, R. 2576 (II, 15), 10471 (I, 7a), 5491 (II, 32) [tipo, *A. persimilis*]. Schimper 1535 (I, 3) [tipo, *A. caudatus* var. *alopecurus*]. Schulz, A. G. 3296 (II, 5d), 14712 (II, 5d), 14709 (II, 29), 2952 (I, 12), 8671 (I, 12), 3861 (II, 43), 3860 (II, 50), 14707 (II, 50). Schwabe, H. 385 (II, 15), 392 (II, 29). Schwarz, G. L. 1621 (I, 7b), 4019 (I, 7b), 4192 (I, 7b), 4659 (I, 7b). Schwindt, E. 75 (I, 7b), 576 (I, 7b), 75 (II, 50). Scott, M. I. H. & M. Birabén 1210 (I, 7b). Seidel, R. 2020 (I, 12). Semper s.n. (II, 23). Senn, H. A. et al. 967 (I, 10). Sennen, F. 4214 (II, 4), 3564 (II, 18c), 4028 (I, 7a), 4030 (I, 7a), 5044 (I, 7a), 6650 (I, 7a), 7440 (I, 7a), s.n. (I, 7a), 5539 (I, 10). Sennen, F. & Jerónimo 7261 (I, 7a). Shinnars, L. H. 30842 (II, 34), 30872 (II, 34), 30814 (II, 41). Shilom Ton, A.

3300 (I, 12). Sickenberger, E. s.n. (I, 7b) [tipo, *A. artineanus*]. Skarpe, C. S-411 (II, 35). Smith, L. B. & S. M. Klein 13105 (I, 7b), 14089 (II, 50). Solís Neffa, V. et al. 286 (II, 38). Soriano, A. 1008 (II, 23). Soto Núñez, J. C. et al. 8004 (I, 12). Specht, R. L. 567 (II, 48). Spegazzini, C. L. s.n. (II, 5b), s.n. (II, 5d), s.n. (I, 2), s.n. (I, 3), s.n. (I, 3) [tipo, *A. edulis*], s.n. (II, 13), s.n. (II, 15) [tipo, *Amarantellus argentinus*], s.n. (II, 15), s.n. (I, 7a), s.n. (I, 7b), s.n. (II, 29), s.n. (I, 12), 167 (II, 43) [tipo, *A. vulgatissimus*], s.n. (II, 43). Stewart, A. 1360 (II, 40) [tipo, *A. sclerantoides* f. *abingdonensis*], 1362 (II, 42). Steyermark, J. A. et al. 122886 (I, 5). Stipieraere, H. B2490 (I, 10). Stutz, L. C. 521 (I, 12). Subils, R. 444 (I, 7b), 445 (I, 7b). Svenson, H. K. 20 (II, 40), 11280 (II, 49). Symon, D. E. 5395 (II, 48), 5412 (II, 48).

Taylor, T. W. J. 136 (I, 5). Tedone 4954 (II, 29). Terribile, M. 635 (II, 43). Tharp, B. C. & F. Barkley 15591 (II, 41). Till, W. 136 (II, 2). Tisdale, E. W. 40-356 (I, 10). Todaro 405 (II, 2). Tollewey, F. E. 103 (I, 12). Tonduz, A. 13704 (I, 11). Torrey 457 (II, 2) [tipo, *Amaranthus graecizans* var. *pubescens*]. Travers s.n. (I, 7a). Townsend, C. C. 73/101 (II, 47). Triana, J. 961 (I, 4). Troncoso, N. et al. 2797 (II, 15), 3572 (I, 7a), 3573 (II, 50). Tún Ortiz, R. 1219 (II, 34). Tuerckheim, H. 8567 (I, 4).

Ulibarri, E. 291 (II, 29).

Valderrama J. 34 (I, 12). Van der Werff, H. H. 2055 (II, 3). Ventura, A. 2209 (II, 1). Venturi, S. 1957 (II, 5d), 98 (I, 7b), 2045 (I, 7b), 4234 (I, 7b), 73 (II, 29), 995 (II, 29), 2438 (II, 29), 2839 (II, 50). Vihodzevsky s.n. (II, 4). Villafañe, M. 615 (I, 7a), 1109 (I, 7a), 1275 (I, 7a), 173 (II, 43), 731 (II, 43). Villamil, C. B. M. G. Cazzaniga 3852 (II, 13). Vyhodcevski, N. 433 (I, 10).

Wang, B. M. 93 (I, 7a). Warren, D. K. & R. M. Turner 68-207 (I, 6). Waterfall, U. T. 6620 (II, 7) [tipo, *Amaranthus microphyllus*]. Wheeler, L. C. 12842 (II, 47). Wheeler Haines, R. 15 (II, 2). Wiggins, I. L. 15598 (I, 6), 18433 (II, 40). Wilman, M. s.n. (II, 35). Wilson, K. L. 1301 (II, 26b). White, S. S. 1999 (II, 4). Williamson, J. s.n. (II, 2), 574 (II, 2), 1115 (II, 13). Wolff, S. E. 40 (II, 34). Wolf & Rothrock 275 (I, 13) [tipo, *A. wrightii*]. Wright, C. 582 (II, 41) [tipo, *A. scleropoides*].

Xena, N. 1019 (I, 5).

Zabala, S. 22 (II, 5b), 564 (II, 23) [tipo, *Amaranthus kloosianus*]. Zardini, E. M. & R. Velásquez 9701 (I, 7b). Zeballos, R. I (I, 4). Zeyher s.n. (II, 8a), s.n. (II, 8a), 1438 (II, 39), s.n. p.p (II, 45). Zobel, A. s.n. (II, 8a) [tipo, *A. capensis* subsp. *capensis*]. Zuloaga, F. O. 24643 (II, 52).

SYNOPSIS OF *ACALYPHA* (EUPHORBIACEAE) OF ARGENTINA, PARAGUAY, AND URUGUAY¹

José María Cardiel² and Pablo Muñoz
Rodríguez³

ABSTRACT

A critical review of the Argentinian, Uruguayan, and Paraguayan species of *Acalypha* L. (Euphorbiaceae) is presented. As a result, 18 species (22 taxa) are accepted, 16 from Argentina, 12 from Paraguay, and five from Uruguay, and 49 names are considered as synonyms. Typifications are provided for *A. brasiliensis* Müll. Arg., *A. cordobensis* Müll. Arg., *A. friesii* Pax & K. Hoffm., *A. gracilis* Spreng., *A. nitschkeana* Pax & K. Hoffm., *A. multicaulis* Müll. Arg. var. *glabrescens* Pax & K. Hoffm., *A. lagoensis* Müll. Arg. var. *grandifolia* Chodat & Hassl., and *A. striolata* Lingelsh. Identification keys are also provided as are original illustrations of three species and distribution maps of all the accepted taxa.

Key words: *Acalypha*, Argentina, Euphorbiaceae, Paraguay, South America, Uruguay.

Acalypha L. is one of the largest genera in the Euphorbiaceae, with ca. 500 species. The genus is mainly pantropical, but some species are found in temperate regions. The New World is home to around two thirds of the species, which are found from southeastern Canada and the United States to Uruguay and northern Argentina. The species are found in a wide variety of habitats, from tropical rainforests to subdesertic areas, and range from sea level to 4000 m in altitude (Cardiel & Muñoz-Rodríguez, 2012). Updated information on the presence of *Acalypha* in the Americas can be found in Cardiel et al. (2013b). The present work continues the ongoing revision of *Acalypha* for South American countries preceded by Cardiel (1995a, 1995b, 1999, 2007, 2010), Cardiel and Muñoz-Rodríguez (2012), and Cardiel et al. (2013b).

Argentinian species of *Acalypha* were studied by Lourteig and O'Donnell (1942, 1943) and updated by Lourteig (1954). They recognized 14 species of *Acalypha* (17 taxa; Table 1) and included excellent illustrations. No relevant changes were introduced in the national catalogue by Bacigalupo and Mulgúra

(1999) or in the catalogue of Euphorbiaceae for the Southern Cone region by Berry et al. (2007). Finally, several regional or thematic floras and checklists also included *Acalypha* species: those from Bianco and Cantero (1992), Bacigalupo (2005), Pensiero et al. (2005), and Tressens et al. (2008). However, Paraguayan and Uruguayan plants are less well known; there are no national floras or checklists that include *Acalypha* species for these countries. In their world treatment of *Acalypha*, Pax and Hoffmann (1924) recognized nine and three species from Paraguay and Uruguay, respectively. In the Southern Cone catalogue, Berry et al. (2007) reported eight and four species from Paraguay and Uruguay, respectively (Table 2). De Egea et al. (2012) reported two species of *Acalypha* from Ñeembucú Department (Paraguay). Also relevant is the recent revision of the species included in *Acalypha* sect. *Communes* Pax & K. Hoffm. ex Cardiel, P. Muñoz & Muñoz Garm. (Cardiel et al., 2013a), which are widespread in the studied countries.

The *Acalypha* species treated in this synopsis are herbs, subshrubs or shrubs, and rarely small trees.

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Table 1. Taxonomic comparison of *Acalypha* L. cited for Argentina by Lourteig and O'Donell (1942) and Lourteig (1954), Berry et al. (2007), and this work. Currently accepted names appear in boldface.

Lourteig & O'Donell (1942) and Lourteig (1954)	Berry et al. (2007)	Cardiel & Muñoz-Rodríguez (2015)
<i>A. amblyodonta</i> (Müll. Arg.) Müll. Arg. var. <i>villosa</i> (Müll. Arg.)	<i>A. amblyodonta</i>	<i>A. amblyodonta</i>
<i>A. boliviensis</i> Müll. Arg.	<i>A. boliviensis</i>	<i>A. boliviensis</i>
<i>A. brasiliensis</i> Müll. Arg.	<i>A. brasiliensis</i>	<i>A. brasiliensis</i>
<i>A. communis</i> Müll. Arg. var. <i>communis</i>	= <i>A. communis</i>	= <i>A. communis</i> subsp. <i>communis</i>
<i>A. communis</i> var. <i>guaranitica</i> Chodat & Hassl.	= <i>A. communis</i>	= <i>A. communis</i> subsp. <i>apicalis</i>
<i>A. communis</i> var. <i>salicifolia</i> Pax & K. Hoffm.	= <i>A. communis</i>	= <i>A. communis</i> subsp. <i>paraguariensis</i>
<i>A. communis</i> var. <i>saltensis</i> Pax & K. Hoffm.	= <i>A. communis</i>	= <i>A. communis</i> subsp. <i>saltensis</i>
		<i>A. communis</i> subsp. <i>tracheliifolia</i>
<i>A. flabellifera</i> Rusby	= <i>A. plicata</i>	= <i>A. plicata</i>
<i>A. friesii</i> Pax & K. Hoffm.	<i>A. friesii</i>	= <i>A. communis</i> subsp. <i>saltensis</i>
<i>A. gracilis</i> Spreng.	<i>A. gracilis</i>	<i>A. gracilis</i>
<i>A. hassleriana</i> Chodat	<i>A. hassleriana</i>	not found in Argentina
<i>A. lycioides</i> Pax & K. Hoffm.	<i>A. lycioides</i>	<i>A. lycioides</i>
<i>A. multicaulis</i> Müll. Arg.	<i>A. multicaulis</i>	<i>A. multicaulis</i>
<i>A. nitschkeana</i> Pax & K. Hoffm.	<i>A. nitschkeana</i>	= <i>A. herzogiana</i>
	<i>A. plicata</i>	<i>A. plicata</i>
<i>A. poiiretii</i> Spreng.	<i>A. poiiretii</i>	<i>A. poiiretii</i>
<i>A. schreiteri</i> Lillo	<i>A. schreiteri</i>	<i>A. schreiteri</i>
		<i>A. senilis</i>
		<i>A. striolata</i>
		<i>A. variabilis</i>
		<i>A. vellamea</i>
<i>A. villosa</i> Jacq.	<i>A. villosa</i>	<i>A. villosa</i>

They are morphologically well characterized by their undivided, alternate, petiolate, stipulate leaves; the inflorescences can be terminal or axillary, frequently both, unisexual or androgynous, and usually spicate (herein, they are only racemose in *A. villosa* Jacq.). The flowers are unisexual and apetalous. The staminate flowers are inconspicuous and similar; the pistillate flowers are small, usually sessile, and subtended by bracts that become foliaceous and accrescent in the fruit. The shape, size, and indumentum of these bracts are taxonomically valuable characters to distinguish species. Only one of the treated species herein, *A. villosa*, has pedicellate flowers with small, non-acrescent bracts. The fruits in *Acalypha* are capsular, 3-lobed, with diverse trichome types that are also useful to distinguish species.

The aim of this work is to present a critical synopsis of the species of *Acalypha* for Argentina, Paraguay, and Uruguay, and to provide taxonomic keys to facilitate their identification. Three original illustrations are included as are synoptic distribution maps for all the accepted species.

MATERIALS AND METHODS

This work is based on the study of 600 collections of *Acalypha* from Argentina, 450 from Paraguay, and

60 from Uruguay. The following herbaria are acknowledged: A, AAU, B, BM, BR, C, CAS, CORD, CTES, DAV, F, G, G-DC, GB, GH, GOET, HAL, HBG, JE, K, L, LIL, M, MA, MO, MPU, NY, P, PR, S, SEL, SI, U, UC, UPS, US, W, WU, Z, and ZT (acronyms according to Thiers, 2011).

The structure of the synopsis generally follows that used in previous works (Cardiel & Muñoz-Rodríguez, 2012; Cardiel et al., 2013b). Only the synonyms based on Argentinean, Uruguayan, and Paraguayan specimens are included along with the names previously cited as accepted for these countries. Any novel designation of type was made after a careful review of the original literature of the taxa and examination of original material. When no holotype was indicated or when it had been lost or destroyed, a lectotype or neotype has been designated, according to the rules of the International Code of Nomenclature (McNeill et al., 2012). Illustrations are cited when available. General geographic distributions for species and infraspecies are provided following Taxonomic Database Working Group standards (Brummitt, 2001) as are detailed Argentinian, Paraguayan, and Uruguayan distributions, which indicate the provinces (for Argentina) or departments (for Paraguay and Uruguay) in which the species have been found in each country. This information is generally based on the studied specimens and, in some cases,

Table 2. Taxonomic comparison of *Acalypha* L. cited for Paraguay and Uruguay by Pax and Hoffmann (1924), Berry et al. (2007), and this work. Currently accepted names appear in boldface.

Paraguay		
Pax & Hoffmann (1924)	Berry et al. (2007)	Cardiel & Muñoz-Rodríguez (2015)
<i>A. amblyodonta</i> (Müll. Arg.) Müll. Arg.	<i>A. amblyodonta</i>	<i>A. amblyodonta</i>
<i>A. brevipes</i> (Müll. Arg.) Müll. Arg.	not cited	= <i>A. vellamea</i>
<i>A. communis</i> Müll. Arg. var. <i>hirta</i> (Spreng.) Müll. Arg.	<i>A. communis</i>	= <i>A. variabilis</i>
<i>A. communis</i> var. <i>intermedia</i> Müll. Arg.	<i>A. communis</i>	= <i>A. communis</i> subsp. <i>communis</i>
<i>A. communis</i> var. <i>tomentella</i> Müll. Arg.	<i>A. communis</i>	= <i>A. communis</i> subsp. <i>communis</i>
<i>A. communis</i> var. <i>tomentosa</i> Müll. Arg.	<i>A. communis</i>	= <i>A. communis</i> subsp. <i>communis</i>
<i>A. flabellifera</i> Rusby	not cited	The voucher cited by Pax and Hoffmann corresponds to <i>A. amblyodonta</i> . <i>Acalypha flabellifera</i> is a synonym of <i>A. plicata</i> Müll. Arg. not found in Paraguay.
<i>A. gracilis</i> Spreng.	<i>A. gracilis</i>	<i>A. gracilis</i>
<i>A. hassleriana</i> Chodat	<i>A. hassleriana</i>	<i>A. hassleriana</i>
<i>A. multicaulis</i> Müll. Arg.	<i>A. multicaulis</i>	<i>A. multicaulis</i>
<i>A. nitschkeana</i> Pax & K. Hoffm.	<i>A. nitschkeana</i>	= <i>A. herzogiana</i>
		<i>A. senilis</i>
		<i>A. striolata</i>
		<i>A. variabilis</i>
	<i>A. vellamea</i>	<i>A. vellamea</i>
<i>A. villosa</i> Jacq.	<i>A. villosa</i>	<i>A. villosa</i>
		<i>A. wilkesiana</i>
Uruguay		
Pax & Hoffmann (1924)	Berry et al. (2007)	Cardiel & Muñoz-Rodríguez (2015)
<i>A. communis</i> var. <i>salicifolia</i> Pax & K. Hoffm.	<i>A. communis</i>	<i>A. communis</i> subsp. <i>tracheliifolia</i>
<i>A. gracilis</i> Spreng.	<i>A. gracilis</i>	<i>A. gracilis</i>
	<i>A. multicaulis</i>	<i>A. multicaulis</i>
<i>A. senilis</i> Baill.	<i>A. senilis</i>	<i>A. senilis</i>
		<i>A. variabilis</i>

on a bibliographic source. This information is also reflected in the distribution maps provided. Biogeographic regions, altitudinal range, and habitat are described. We follow the natural regions proposed by Zuloaga et al. (2008) for the South American Southern Cone. Finally, we list recent literature that provides updated information about the species.

All information gathered as part of this work is available online on the regularly updated *Acalypha* Taxonomic Information System web site, <www.acalypha.es> (Cardiel et al., 2015). In addition, specimen detail has been uploaded to the Global Biodiversity Information Facility (GBIF) (2015) at <http://www.gbif.org/dataset/search?q=12046>.

RESULTS

We recorded 67 scientific names related to *Acalypha* from Argentina, Paraguay, and Uruguay, 18 of which are accepted species names, 16 of which are present in Argentina, 12 in Paraguay, and five in Uruguay (Tables 1, 2). Forty-nine names are considered synonyms. We indicate the type speci-

men(s) for each of the valid names, and we designate seven lectotypes and one neotype. Two species are endemics, *A. schreiteri* Lillo ex Lourteig & O'Donell from Argentina and *A. hassleriana* Chodat from Paraguay, and one species is introduced, *A. wilkesiana* Müll. Arg. We treat two of the 14 species recognized by Lourteig and O'Donell (1942, 1943, 1954) for Argentina as synonyms: *A. friesii* Pax & K. Hoffm. and *A. nitschkeana* Pax & K. Hoffm. (also treated for Paraguay by Berry et al., 2007). Another species, *A. hassleriana*, is based on a misidentification, and we have excluded it. We also report four species new for Argentina: *A. senilis* Baill., *A. striolata* Lingelsh., *A. variabilis* Klotzsch ex Baill., and *A. vellamea* Baill. (Table 1). For Paraguay, we add four species never before cited for this country, *A. senilis*, *A. striolata*, *A. variabilis*, and *A. wilkesiana*, in addition to all of the species recognized by Berry et al. (2007); one of them, *A. nitschkeana*, is treated as a synonym of *A. herzogiana* Pax & K. Hoffm. Finally, for Uruguay, we add one species, *A. variabilis*, to the four recognized by Berry et al. (2007) (Table 2). The southern boundary of the distribution of *Acalypha* in

South America is located in northern Argentina and Uruguay. It was outlined by Lourteig and O'Donell (1942), and now, after studying the distribution of the genus in these countries and together with the previous revision from Peru and Bolivia (Cardiel et al., 2013b), we are able to more precisely define the southern extent of the genus in South America.

I. *Acalypha* L., Sp. Pl. 2: 1003. 1753. TYPE:
Acalypha virginica L. (lectotype, designated by Small, 1913: 457).

Ia. *Acalypha* subg. *Acalypha*

Geographically included species (17). *Acalypha amblyodonta* (Müll. Arg.) Müll. Arg., *A. boliviensis* Müll. Arg., *A. brasiliensis* Müll. Arg., *A. communis*

Müll. Arg., *A. gracilis* Spreng., *A. hassleriana*, *A. herzogiana*, *A. lycioides* Pax & K. Hoffm., *A. multicaulis* Müll. Arg., *A. plicata* Müll. Arg., *A. poiretii* Spreng., *A. schreiteri*, *A. senilis*, *A. striolata*, *A. variabilis*, *A. vellamea*, and *A. wilkesiana*.

Ib. *Acalypha* subg. *Linostachys* (Klotzsch ex Schltdl.) Pax & K. Hoffm. Pflanzenr. (Engler) 147, 16(Heft 85): 13. 1924. Basionym: *Linostachys* Klotzsch ex Schltdl., Linnaea 19: 235. 1846. TYPE: *Linostachys padifolia* Schltdl., Linnaea 19: 235. 1846. [= *Acalypha schlechten-daliana* Müll. Arg.].

Geographically included species (1). *Acalypha villosa*.

KEY TO THE SPECIES OF *ACALYPHA* OF ARGENTINA, PARAGUAY, AND URUGUAY

- 1a. Pistillate flowers pedicellate; calyx with 4 or 5 sepals, the subtending bracts inconspicuous, not becoming foliaceous in fruit (*Acalypha* subg. *Linostachys*) 17. *A. villosa* Jacq.
- 1b. Pistillate flowers sessile; calyx with 3 sepals, the subtending bracts becoming foliaceous and accrescent in fruit (*Acalypha* subg. *Acalypha*).
 - 2a. Inflorescences staminate and androgynous, then mostly staminate with one to several pistillate flowers at the base.
 - 3a. Staminate inflorescences terminal; glandular trichomes absent 9. *A. multicaulis* Müll. Arg.
 - 3b. Staminate inflorescences axillary; glandular trichomes present or absent.
 - 4a. Leaf blades broadly ovate, palmately nerved; glandular trichomes present.
 - 5a. Young branches, leaves, and inflorescences covered with conspicuous glandular trichomes 10. *A. plicata* Müll. Arg.
 - 5b. Glandular trichomes usually present only on inflorescences, sometimes also a few on young branches 1. *A. amblyodonta* (Müll. Arg.) Müll. Arg.
 - 4b. Leaf blades narrowly ovate-lanceolate or elliptic-lanceolate, pinnately or pinnipalmately nerved; glandular trichomes absent.
 - 6a. Leaf blades with stellate trichomes 3. *A. brasiliensis* Müll. Arg.
 - 6b. Leaf blades without stellate trichomes.
 - 7a. Leaf blades narrowly elliptic-lanceolate, up to 4.5(–5) cm long; accrescent pistillate bracts suborbicular-reniform, teeth minute, equal 8. *A. lycioides* Pax & K. Hoffm.
 - 7b. Leaf blades ovate or ovate-lanceolate, up to 12 cm long; accrescent pistillate bracts ovate-lanceolate, teeth conspicuous, central one largest 12. *A. schreiteri* Lillo ex Lourteig & O'Donell
 - 2b. Inflorescences unisexual or rarely some inflorescences androgynous, then mostly pistillate with a distal segment of staminate flowers.
 - 8a. Staminate inflorescences terminal, at least in part.
 - 9a. Rhizomatous herbs, sometimes with slightly woody base; pistillate flowers in spikes and some pistillate flowers solitary, axillary, without developed bract 7. *A. herzogiana* Pax & K. Hoffm.
 - 9b. Shrubs or herbs not rhizomatous (slightly rhizomatous in *A. gracilis*); pistillate flowers always in spikes; solitary pistillate flowers absent.
 - 10a. Leaf blades membranous, sparsely pubescent on upper and lower surface, margin dentate 5. *A. gracilis* Spreng.
 - 10b. Leaf blades chartaceous, glabrous or with some appressed hairs on midrib, margin entire to obscurely dentate 14. *A. striolata* Lingelsh.
 - 8b. Staminate inflorescences all axillary.
 - 11a. Pistillate inflorescences all axillary 18. *A. wilkesiana* Müll. Arg.
 - 11b. Pistillate inflorescences terminal, at least in part.
 - 12a. Herbs, annual but sometimes the base becoming somewhat woody; pistillate inflorescences densely flowered, the axis not conspicuously visible.
 - 13a. Inflorescences pistillate or androgynous (mostly pistillate with a distal segment of staminate flowers), ellipsoid; pistillate bracts with the terminal tooth usually longer than the others 11. *A. poiretii* Spreng.
 - 13b. Inflorescences all unisexual, pistillate, cylindrical; pistillate bracts with equal tooth 2. *A. boliviensis* Müll. Arg.

- 12b. Shrubs or subshrubs, perennial; pistillate inflorescences not densely flowered, with the axis conspicuously visible.
- 14a. Young branches and leaf blades with numerous glandular trichomes; leaf blades usually deeply cordate at base 6. *A. hassleriana* Chodat
- 14b. Young branches and leaf blades usually without glandular trichomes (a few in *A. communis* subsp. *trachelifolia* (Pax & K. Hoffm.) Cardiel & P. Muñoz); leaf blades rounded or rarely slightly cordate at base.
- 15a. Accrescent pistillate bracts with glandular trichomes; leaf blades usually with conspicuous bright, resinous droplets 4. *A. communis* Müll. Arg.
- 15b. Accrescent pistillate bracts without glandular trichomes; leaf blades with or without bright, resinous droplets.
- 16a. Young branches usually hispid; leaf blades usually conduplicate, glabrous or subglabrous (with appressed trichomes on veins); lower leaf surface covered by a bright exudate, sometimes reduced to spots 15. *A. variabilis* Klotzsch ex Baill.
- 16b. Young branches tomentose to velutinous; leaf blades not conduplicate (sometimes slightly conduplicate in *A. senilis*), \pm densely velutinous; lower leaf surface without exudate.
- 17a. Leaf subsessile or with petioles to 3(–5) mm long, blades elliptic to oblong-lanceolate, chartaceous 16. *A. vellamea* Baill.
- 17b. Leaf with petioles to (5–)10–50 mm long, blades ovate-triangular to subrounded, membranous 13. *A. senilis* Baill.

TAXONOMIC SYNOPSIS

1. *Acalypha amblyodonta* (Müll. Arg.) Müll. Arg., Fl. Bras. 11(2): 365. 1874. Basionym: *Acalypha cuspidata* Jacq. var. *amblyodonta* Müll. Arg., Linnaea 34: 37. 1865. *Ricinocarpus amblyodontus* (Müll. Arg.) Kuntze, Revis. Gen. Pl. 2: 618. 1891. TYPE: [Brazil. Rio de Janeiro]: in Brasilia prope Rio de Janeiro, 1833, C. Gaudichaud 1134 (lectotype, designated by Cardiel et al., 2013b: 155, P [barcode P00635211!]; isoelectotypes, B† [B neg. F 5277!], G-DC!).

Acalypha lagoensis Müll. Arg. var. *grandifolia* Chodat & Hassl., Bull. Herb. Boissier, sér. 2, 5: 604. 1895. TYPE: [Paraguay. Paraguari]: in silvis pr. Caraguaty, Oct., E. Hassler 3322 (lectotype, designated here, P [barcode P00635281!]; isoelectotypes, BM!, F!, GH!, K!, P!, W!).

Iconography. Lourteig and O'Donnell (1942: 299, fig. 6; 1943: tab. 93b), sub. *Acalypha amblyodonta* var. *villosa* Müll. Arg.

Distribution. *Acalypha amblyodonta* is known from Brazil (Cardiel, 2010), Bolivia (Cardiel et al., 2013b), northern Argentina, and Paraguay. In Argentina, five collections were examined from the provinces of Jujuy and Salta. The species has been collected in Paraguay from the departments of Alto Paraguay, Central, Paraguari, and Presidente Hayes (seven collections examined). *Acalypha amblyodonta* extends into the Chaco and north-central Wet Andes regions and has been collected from elevations of 100–500 m, frequently along riversides (Fig. 1A).

References. Berry et al. (2007), Cardiel (2010), Cardiel et al. (2013b).

Notes. Bacigalupo and Mulgura (1999) cited *Acalypha amblyodonta* from Misiones Province (Argentina), but this was based on the collection A. P. Rodrigo 1040 (NY), which taxonomically corresponds to *A. multicaulis*. We did not find *A. amblyodonta* in Misiones Province. *Acalypha amblyodonta* is morphologically close to *A. plicata*, but the latter is easily distinguishable by the presence of conspicuous glandular trichomes that cover leaves and inflorescences. In *A. amblyodonta* the glandular trichomes are only present on the inflorescences; sometimes also a few trichomes are observed on young branches.

The synonym *Acalypha lagoensis* var. *grandifolia* was described as based on a single collection, E. Hassler 3322, of which we have found seven duplicates. Due to the lack of a holotype indication, we selected the best preserved specimen, from the P herbarium, as lectotype.

Selected specimens examined. ARGENTINA. **Jujuy:** Dpto. Ledesma, confluencia río Piedras y Arroyo Pantanoso, 500 m, 17 Apr. 1968, C. Fabris 7313 (P). **Salta:** Orán, quebrada del Anta Muerta, 7 Dec. 1972, V. Maruñak et al. 481 (MO). PARAGUAY. **Alto Paraguay:** ad ripam occidentalem flum. Paraguay, Oct. 1903, E. Hassler 2383 (BM, GH, K, NY, W). **Central:** L'Asumption, pres du Cerro Tacumbu, May 1874, B. Balansa 1696 (BM, K). **Paraguari:** in silva Caraguaty, E. Hassler 3322 (BM, F, GH, K, W). **Presidente Hayes:** Puerto Militar, Estancia Casuariaga, 9 Dec. 1989, R. Vanni et al. 1241 (MO).

2. *Acalypha boliviensis* Müll. Arg., Linnaea 34: 162. 1865. *Ricinocarpus boliviensis* (Müll. Arg.) Kuntze, Revis. Gen. Pl. 2: 617. 1891. TYPE: [Bolivia. La Paz]: Prov. Larecaja, Sorata, 1858–1859, G. Mandon 1070 (holotype, G-DC [barcode G00324655!]; isotypes, B† [B neg. F

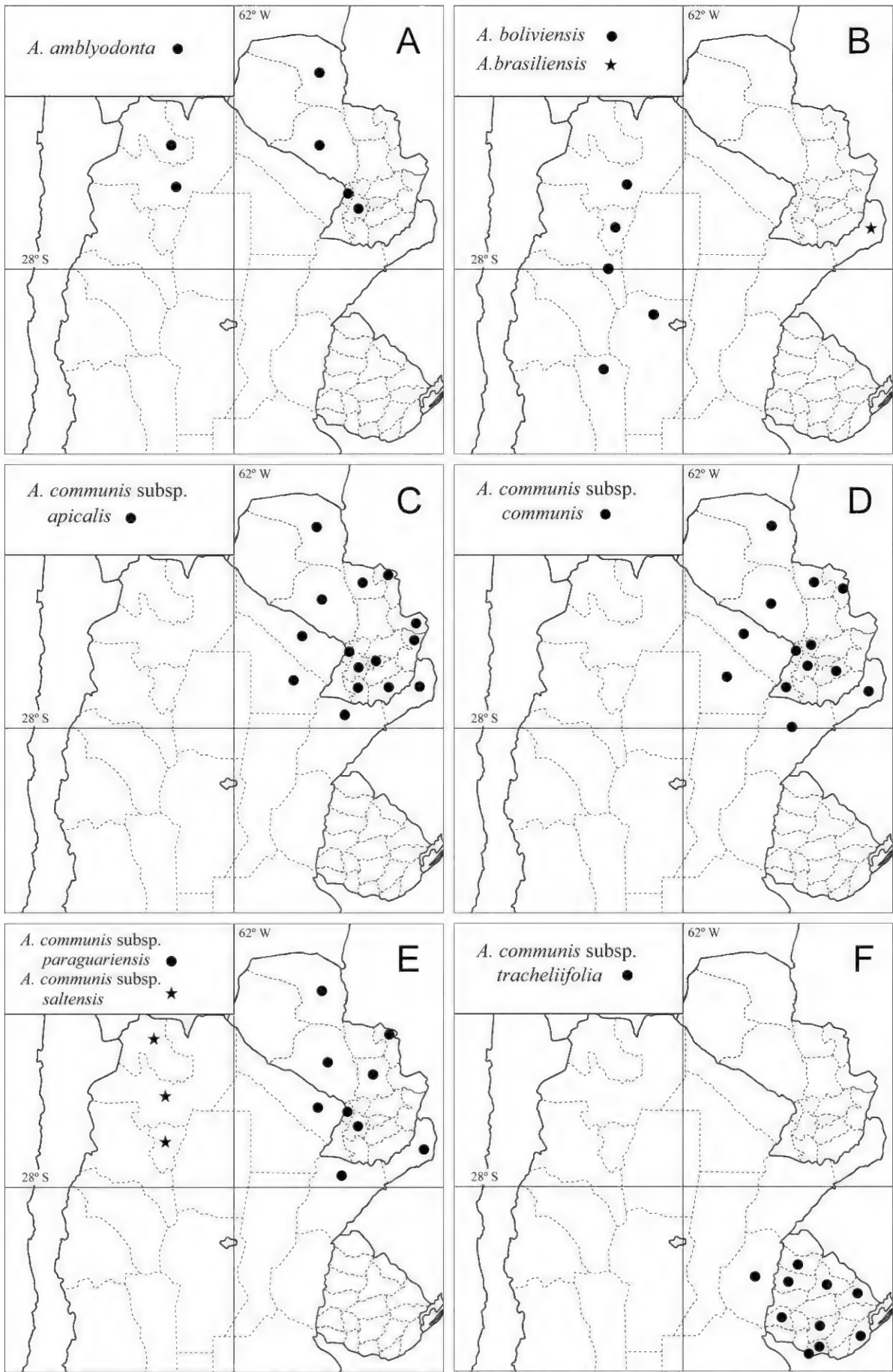


Figure 1. Maps showing distributions in Argentina, Paraguay, and Uruguay of selected *Acalypha* species. —A. *Acalypha amblyodonta* (Müll. Arg.) Müll. Arg. —B. *Acalypha boliviensis* Müll. Arg. and *A. brasiliensis* Müll. Arg. —C. *Acalypha communis* Müll. Arg. subsp. *apicalis* (N. E. Br.) Cardiel & P. Muñoz. —D. *Acalypha communis* subsp. *communis*. —E. *Acalypha communis* subsp. *paraguariensis* (Chodat & Hassl.) Cardiel & P. Muñoz and *A. communis* subsp. *saltensis* (Pax & K. Hoffm.) Cardiel & P. Muñoz. —F. *Acalypha communis* subsp. *trachelifolia* (Pax & K. Hoffm.) Cardiel & P. Muñoz.

5285!], G!, F [2!], K!, M!, NY [2!], P [3!], S [2!], W!).

Iconography. Lourteig and O'Donnell (1942: 301, fig. 7; 1943: tab. 86).

Distribution. *Acalypha boliviensis* is known from Bolivia (Cardiel et al., 2013b) and Argentina. In Argentina, the species has been found in the provinces of Catamarca, Córdoba, Salta, San Luis, and Tucumán (six collections examined). This species extends into the north-central Wet Andes

region and has been collected from elevations of 1300–2000 m (Fig. 1B).

References. Berry et al. (2007), Cardiel et al. (2013b).

Notes. *Acalypha boliviensis* is sometimes confused with the widely distributed *A. poiretii* because of their herbaceous habits. However, *A. boliviensis* is easily distinguishable by its cylindrical unisexual inflorescences and pistillate bracts with broadly triangular teeth, with the central tooth usually much longer than the others, versus the inflorescences ellipsoid, pistillate or androgynous, and pistillate bracts with narrowly triangular and equal-sized teeth in *A. poiretii*.

Selected specimens examined. ARGENTINA. **Catamarca:** Bacigalupo & Mulgúra (1999). **Córdoba:** Bacigalupo & Mulgúra (1999). **Salta:** Dpto. La Merced. Finca El Rodeo, 17 May 1983, *J. L. Novara 3415* (MO). **San Luis:** Dpto. Junín, Sierra de Comechingones, subiendo desde El Rincón, 8 Feb. 1956, *A. T. Hunziker 11737* (CORD, MA, MBM). **Tucumán:** Siambon (Dpto. Tafí), 1300 m, 5 Feb. 1933, *L. R. Parodi 11053* (GH).

3. *Acalypha brasiliensis* Müll. Arg., Linnaea 34: 37. 1865. *Acalypha brasiliensis* var. *mollis* Müll. Arg., Linnaea 34: 37. 1865. *Acalypha dupraeana* var. *arciana* Baill., Adansonia 5: 230. 1865, nom. illeg. superfl. *Ricinocarpus brasiliensis* (Müll. Arg.) Kuntze, Revis. Gen. Pl. 2: 617. 1891. TYPE: Brazil. Bahia: Pongo d’Arcia, June 1844, *J. S. Blanchet 3865* (lectotype, designated here, G-DC [barcode G00324483!]; isoelectotypes, BM!, G [3]!, P!).

Iconography. Lourteig and O’Donell (1942: 303, fig. 8; 1943: tab 87).

Distribution. *Acalypha brasiliensis* is known from Brazil (Cardiel, 2010) and northeastern Argentina. In Argentina, 12 collections from the province of Misiones were examined. This species extends into the Atlantic Forest region and is collected from elevations of 150 to 400 m, frequently along riversides (Fig. 1B).

Reference. Berry et al. (2007).

Notes. *Acalypha brasiliensis* was first described by Müller Argoviensis in March 1865 in the journal *Linnaea*. He divided the species into three varieties: *Acalypha* [var.] α *mollis*, *Acalypha* [var.] β *asterotricha* (additionally divided into two forms: *Acalypha* [f.] *a cordata*, *Acalypha* [f.] *b obtusa*), and *Acalypha* [var.] δ *psilophylla*. Müller Argoviensis added an additional four varieties in 1874 (*Acalypha brasiliensis*

var. *brevipes* Müll. Arg., *A. brasiliensis* var. *glabrata* Müll. Arg., *A. brasiliensis* var. *longipes* Müll. Arg., and *A. brasiliensis* var. *maxima* Müll. Arg.). In order to fix the application of the name *A. brasiliensis*, it is lectotypified using original material of *A. brasiliensis* var. *mollis* because we consider it to be representative of the species and the type specimens are well preserved. The other varieties, all based on Brazilian plants, are still under review.

The conspecific name *Acalypha dupraeana* var. *arciana* was published by Baillon in April–May 1865, in the journal *Adansonia*, referencing the same collection used before by Müller Argoviensis (in March 1865) to describe *A. brasiliensis* var. *mollis* (*M. Blanchet 3865*); therefore Baillon’s name must be considered a nomenclaturally superfluous illegitimate name (Art. 52.1 of ICN, McNeill et al., 2012). *Acalypha brasiliensis* is widely distributed in southeastern Brazil, and only a few collections are found outside of this country, but the species does occur in the province of Misiones (Argentina). This is the only species in the studied area with stellate trichomes that are found mainly on leaf blades.

Selected specimens examined. ARGENTINA. **Misiones:** Dpto. San Pedro, El Alcázar, 30 Mar. 1949, *E. Schwindt 1428* (K, W); Dpto. San Javier, Santa Ana, 28 Feb. 1947, *G. J. Schwarz 4218* (C, LIL, W).

4. *Acalypha communis* Müll. Arg., Linnaea 34: 23. 1865. *Acalypha communis* Müll. Arg. var. *tomentosa* Müll. Arg., Linnaea 34: 24. 1865. *Ricinocarpus communis* (Müll. Arg.) Kuntze, Revis. Gen. Pl. 2: 617. 1891. TYPE: [Brazil.] In Brasiliae prov. Minarum Generalium, s.d., *J. F. Widgren s.n.* (lectotype, designated by Cardiel et al., 2013a: 1299, S S07-12617!; isoelectotype, BR-699782!).

Iconography. See subspecies.

Distribution. *Acalypha communis* is known from Bolivia (Cardiel et al., 2013b), Brazil (Cardiel, 2010), northern Argentina, Paraguay, and Uruguay. It is found in the Atlantic Forest, Pampas, and north-central Wet Andes regions, collected from elevations of sea level to 1200(–1400) m (Fig. 1C–F).

References. Bacigalupo (2005), Cardiel et al. (2013a, 2013b).

Notes. According to the recent revision of *Acalypha* sect. *Communes* (Cardiel et al., 2013a), *A. communis* is divided into five subspecies widespread in the north of the Southern Cone. All

are present in the studied area. As indicated for Bolivian specimens of *A. communis* (Cardiel et al., 2013b), some specimens have mixed characters that make it difficult to assign them to subspecies. We think that subspecies can hybridize in areas where

they coexist, but further study is required. Lourteig and O'Donnell (1942) cited *A. communis* from Santa Fe Province (Argentina) based on specimen S. Venturi 276 (BA, LIL), which is here identified as *A. variabilis*.

KEY TO THE SUBSPECIES OF *ACALYPHA COMMUNIS*

- 1a. Leaf blades broadly ovate or ovate-lanceolate, (3–)4–9 cm wide.
 - 2a. Young branches and leaf blades velutinous; leaf blades 6–8 × (3–)4–5 cm; petioles 3–5 cm long; resinous droplets usually present on leaves or inflorescences 4a. *A. communis* Müll. Arg. subsp. *communis*.
 - 2b. Young branches and leaf blades puberulous; leaf blades (9–)13–17 × (4–)6–9 cm; petioles (4–)8–19 cm long; resinous droplets present or absent on leaves or inflorescences.
 - 3a. Leaf blades subchartaceous; petioles 4–5(–10) cm long; young branches hispid; resinous droplets present 4b. *A. communis* subsp. *apicalis* (N. E. Br.) Cardiel & P. Muñoz
 - 3b. Leaf blades thinly membranous; petioles 6–14(–19) cm long; young branches puberulous, soon glabrescent; resinous droplets usually absent 4d. *A. communis* subsp. *saltensis* (Pax & K. Hoffm.) Cardiel & P. Muñoz
- 1b. Leaf blades narrowly oblong-lanceolate, 1.5–3 cm wide.
 - 4a. Young branches and leaf blades with minute sparse glandular trichomes; petioles (2–)3–6 cm long; leaf bases truncate to subcordate 4e. *A. communis* subsp. *tracheliiifolia* (Pax & K. Hoffm.) Cardiel & P. Muñoz
 - 4b. Young branches and leaf blades without glandular trichomes; petioles 0.5–1.5(–2) cm long; leaf bases obtuse to rounded 4c. *A. communis* subsp. *paraguariensis* (Chodat & Hassl.) Cardiel & P. Muñoz

4a. *Acalypha communis* subsp. *communis*.

Acalypha agrestis Morong ex Britton, Ann. New York Acad. Sci., 7: 225. 1893. *Acalypha communis* Müll. Arg. var. *agrestis* (Morong ex Britton) Chodat & Hassl., Bull. Herb. Boissier, sér. 2, 1: 397. 1901. TYPE: Paraguay. Central Paraguay, June 1894, *T. Morong* 1578 (lectotype, designated by Cardiel et al., 2013a: 1299, NY [barcode 246087!]; isoelectotypes, K!, NY!, US!).

Iconography. Lourteig and O'Donnell (1942: 305, fig. 9; 1943: tab 88b); Bacigalupo (2005: 174, fig. 84).

Distribution. *Acalypha communis* subsp. *communis* is known from Bolivia (Cardiel et al., 2013b), Brazil (Cardiel, 2010), northeastern Argentina, and Paraguay. In Argentina, 73 collections were examined from the provinces of Chaco, Corrientes, Formosa, and Misiones. In Paraguay, 58 collections were examined from the departments of Alto Paraguay, Amambay, Boquerón [Nueva Asunción], Caazapá, Central, Concepción, Cordillera, Ñeembucú, Paraguairí, and Presidente Hayes. *Acalypha communis* subsp. *communis* extends into the Chaco and Atlantic Forest regions and has been collected from elevations of 100 to 500 m (Fig. 1D).

References. Bacigalupo (2005), Cardiel et al. (2013a, 2013b).

Selected specimens examined. ARGENTINA. **Chaco:** Fontana (Resistencia), 19 Apr. 1967, *A. G. Schulz* 15928 (C, F, MO). **Corrientes:** Dpto. General Paz Pueblo (cercanías), 16 Oct. 1945, *T. Ibarrola* 3535 (C, K, W). **Formosa:** Dpto. Pilcomayo, al Norte de El Porteño, 14 Apr. 1947, *J. Morel*

2503 (LIL, W). **Misiones:** Corrientes, bank on the Río Paraná, 20 Apr. 1956, *T. M. Pedersen* 3884 (C, GH, K, MO, NY). PARAGUAY. **Alto Paraguay:** Siete Puntas, May 1917, *T. Rojas* 2677 (GH). **Amambay:** Sierra de Amambay, June 1912–1913, *E. Hassler* 11242a (BM, G, GH, K, NY, W). **Boquerón [Nueva Asunción]:** Nueva Asunción, Apr. 1875, *B. Balansa* 1698 (K). **Caazapá:** Tavai, Bosque del Dpto. Militar, 17 Mar. 1989, *I. Basualdo* 2337 (MO). **Central:** Laguna Ypacarai, 4 Mar. 1903, *K. Fiebrig* 959 (BM, F, GH). **Concepción:** Concepción, 21 Mar. 1980, *E. Purvey* 96 (MO). **Cordillera:** Cerro Zanja Jhú, 25 June 1988, *E. Zardini* 5131 (F, MO [2]). **Ñeembucú:** Ñeembucú, Estancia Redondo, 25 Jan. 2005, *J. De Egea Juvinel* 686 (BM). **Paraguairí:** Macizo Acahay, 500 m, 14 July 1988, *E. Zardini* 5783 (F, MO). **Presidente Hayes:** Cerrito, cercanías del Río Verde, 25 May 1987, *E. Zardini* 2643 (MO).

4b. *Acalypha communis* subsp. *apicalis* (N. E. Br.) Cardiel & P. Muñoz, Taxon 62(6): 1299. 2013. Basionym: *Acalypha apicalis* N. E. Br., Trans. & Proc. Bot. Soc. Edinburgh 20: 70. 1894. TYPE: Argentina. Río Pilcomayo, Nov. 1894, *J. G. Kerr* s.n. (holotype, K [barcode K000600553!]). Figure 3.

Acalypha communis f. *longipetiolata* Chodat & Hassl., Bull. Herb. Boissier, sér. 2, 5: 604. 1905. TYPE: [Paraguay.] In campo pr. flumen Jejui guazu, Dec., *E. Hassler* 5705a (holotype, W!).

Acalypha communis var. *guaranitica* Chodat & Hassl., Bull. Herb. Boissier, sér. 2, 5: 605. 1905. TYPE: [Paraguay.] In campis pr. flumen Jejuy guazú, Dec., *E. Hassler* 5705 (lectotype, designated by Cardiel et al., 2013a: 1299, S-07-12619!; isoelectotypes, MA!, P!, UC!, W!).

Acalypha communis f. *grandifolia* Chodat & Hassl., Bull. Herb. Boissier, sér. 2, 5: 605. 1905. TYPE: Paraguay. In silvis in regione cursus superioris fluminis Apa, Jan., *E. Hassler* 8377 (lectotype, designated by Cardiel et al.,

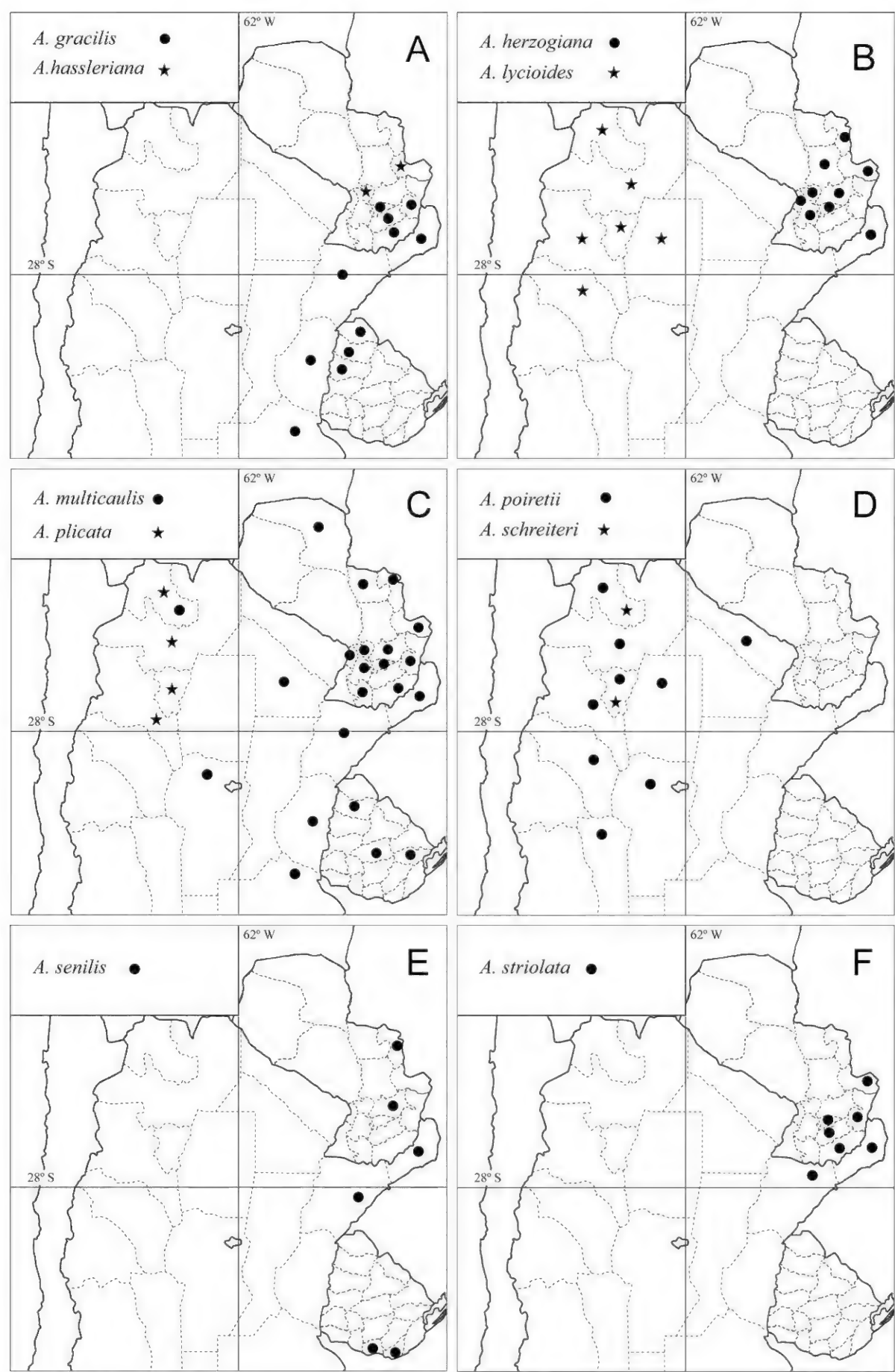


Figure 2. Maps showing distributions in Argentina, Paraguay, and Uruguay of selected *Acalypha* species. —A. *Acalypha gracilis* Spreng. and *A. hassleriana* Chodat. —B. *Acalypha herzogiana* Pax & K. Hoffm. and *A. lycioides* Pax & K. Hoffm. —C. *Acalypha multicaulis* Müll. Arg. and *A. plicata* Müll. Arg. —D. *Acalypha poiretii* Spreng. and *A. schreiteri* Lillo ex Lourteig & O'Donell. —E. *Acalypha senilis* Baill. —F. *Acalypha striolata* Lingelsh.

2013a: 1300, BM [barcode BM000504483]!; isoelecto-type, NY!).

Iconography. Figure 3 herein.

Distribution. *Acalypha communis* subsp. *apicalis* is known from Brazil, northeastern Argentina, and Paraguay. In Argentina, 17 collections were examined from the provinces of Corrientes, Formosa, and

Misiones. In Paraguay, 23 collections were examined from the departments of Alto Paraguay, Alto Paraná, Amambay, Boquerón [Nueva Asunción], Canindeyú, Central, Concepción, Guairá, Itapúa, Misiones, Paraguari, and Presidente Hayes. *Acalypha communis* subsp. *apicalis* extends into the Chaco and Atlantic Forest regions and has been collected from elevations of 50–300 m (Fig. 1C).

References. Bacigalupo (2005) as *Acalypha communis* var. *guaranitica*, Cardiel et al. (2013a, 2013b).

Notes. *Acalypha communis* subsp. *apicalis* can be distinguished from the autonymic subspecies mainly by its broadly ovate or ovate to lanceolate leaf blades up to 17×9 cm. The known distributional area of this subspecies is similar to that of *A. communis* subsp. *communis*, which presents leaf blades up to 8×5 cm. Specimens with intermediate characters can also be found.

Selected specimens examined. BRAZIL. **Mato Grosso:** Brasíliæ civit, Corumbá, 4 Apr. 1903, *A. Malme* 3039 (S). ARGENTINA. **Corrientes:** Dpto. Empedrado, Estancia Las Tres Marías, 31 Mar. 1957, *P. M. Pedersen* 4530 (C, K, MO, NY). **Formosa:** Río Pilcomayo, 1890–1901, *G. Kerr s.n.* (K 600553). **Misiones:** Río Paraná, Puerto La Libertad, 28 Nov. 1978, *L. Bernardi* 18873 (BM, F, MO, NY). PARAGUAY. **Alto Paraguay:** Dpto. San Pedro, Primavera, 19 June 1954, *A. L. Woolston* 235 (K, NY). **Alto Paraná:** cerca del pueblo de Hernandarias, 300 m, 31 Jan. 1982, *J. Fernández-Casas & J. Molero* 5692 (NY). **Amambay:** Parque Nac. Cerro Corá, 13 Feb. 1982, *J. C. Solomon et al.* 6911 (MO). **Boquerón [Nueva Asunción]:** Asunción, Mar. 1943, *Rojas-Pravetti* 10404 (GH). **Canindeyú:** Iter ad Yerbales montium, Sierra de Maracayú, Dec., *E. Hassler* 5705 (BM, GH, MA, NY, W). **Central:** ad ripam, lacus Ypacarai, 1898–1900, *E. Hassler* 3660 (BM, GH, K, MA, NY, W). **Concepción:** Zwischen rio Apa und rio Aquidaban, 29 July 1910, *K. Fiebrig* 4404 (BM, K). **Guairá:** Itangu, près de Villa-Rica, 17 Feb. 1876, *B. Balansa* 2543 (K). **Itapúa:** opposite Puerto Piray, 200 m, 23 Oct. 1978, *S. A. Renvoize* 3227 (C, K, MO, NY). **Misiones:** Santiago, Estancia La Soledad, 23 Dec. 1969, *T. M. Pedersen* 9552 (C, NY). **Paraguarí:** Cesta, Cerro Palacios, 12 Jan. 1988, *M. Ortiz* 429 (MA, MO). **Presidente Hayes:** Dpto. Pilar, Localidad Espinillo, cerca de Puesto Naranjito, 13 Dec. 1950, *T. Meyer* 16021 (W).

4c. *Acalypha communis* subsp. *paraguariensis* (Chodat & Hassl.) Cardiel & P. Muñoz, Taxon 62: 1300. 2013. Basionym: *Acalypha paraguariensis* Chodat & Hassl., Bull. Herb. Boissier, sér 2, 5: 606. 1905. TYPE: [Paraguay.] In dumetis in regione cursus superioris fluminis Apa, Nov., *E. Hassler* 7973 (lectotype, designated by Cardiel et al., 2013a: 1300, NY 246132!; isoelectotypes, BM!, NY!).

Acalypha communis var. *salicifolia* Pax & K. Hoffm. Pflanzenr. (Engler) 147, 16(Heft 85): 39. 1924. TYPE: Argentina. Misiones: Posada S. Ignacio, 14 Jan. 1908, *E. L. Ekman* 475 (lectotype, designated by Cardiel et al., 2013a: 1300, S S-R-7769!; isoelectotype, S S07-12622!).

Iconography. Lourteig and O'Donell (1943: tab 89b), sub. *Acalypha communis* var. *salicifolia*.

Distribution. *Acalypha communis* subsp. *paraguariensis* is known from northeastern Argentina and

Paraguay. In Argentina, 10 collections were examined from the provinces of Corrientes, Formosa, and Misiones. In Paraguay, nine collections were examined from the departments of Alto Paraguay, Amambay, Central, Paraguarí, Presidente Hayes, and San Pedro. *Acalypha communis* subsp. *paraguariensis* extends in the Chaco region, collected from elevations of 100–200 m (Fig. 1E).

Reference. Cardiel et al. (2013a).

Notes. *Acalypha communis* subsp. *paraguariensis* can be mainly distinguished by its narrowly oblong to lanceolate leaf blades, 1.5–3 cm wide. It can be misidentified as *A. communis* subsp. *trachelifolia*, but the distributional areas of the two species do not overlap (see Fig. 1E, F). Detailed differences between the two subspecies can be found in the Key to Species.

Selected specimens examined. ARGENTINA. **Corrientes:** Apóstoles, San José, 19 Feb. 1946, *M. S. Bertoni* 2721 (F, K). **Formosa:** Mojón de Hierro, 7 Jan. 1945, *A. Krapovickas* 1055 (NY). **Misiones:** Dpto. Ituzaingo, Isla Apipé Grande, Puerto San Antonio, 8 Dec. 1973, *A. Krapovickas* 23803 (G, P). PARAGUAY. **Alto Paraguay:** Gran Chaco: Loma Clavel, Nov. 1903, *E. Hassler* 2576 (BM, K, W). **Amambay:** in regione cursus superioris fluminis Apa, Nov. 1901–1902, *E. Hassler* 7973 (BM, NY [2]). **Central:** Central Paraguay, 1888–1890, *T. Morong* 189 (MO, NY). **Paraguarí:** Macizo Acahay, 500 m, 11 June 1988, *E. Zardini* 4728 (F, MO). **Presidente Hayes:** Estancia Santa Asunción, 20 Oct. 2004, *J. De Egea Juvinel* 617 (BM). **San Pedro:** Estancia Carumbé, Distr. Lima, 22 Nov. 1969, *T. M. Pedersen* 9394 (C).

4d. *Acalypha communis* subsp. *saltensis* (Pax & K. Hoffm.) Cardiel & P. Muñoz, Taxon 62: 1300. 2013. Basionym: *Acalypha communis* var. *saltensis* Pax & K. Hoffm. Pflanzenr. (Engler) 147, 16(Heft 85): 39. 1924. TYPE: [Argentina. Salta]: San José, Ufergebüsch, 1872, *P. G. Lorentz & Hieronymus* 259 (lectotype, designated by Cardiel et al., 2013a: 1300, K!; isoelectotype, CORD!).

Acalypha friesii Pax & K. Hoffm. Pflanzenr. (Engler) 147, 16(Heft 85): 50. 1924, syn. nov. TYPE: Argentina. Jujuy: Laguna de la Brea, 15 June 1901, *R. E. Fries* 178 (lectotype, designated here, S S07-12613!; isoelectotypes, K!, S!).

Iconography. Lourteig and O'Donell (1943: tab. 88a).

Distribution. *Acalypha communis* subsp. *saltensis* is known from Bolivia (Cardiel et al., 2013b) and northwestern Argentina. In Argentina, 39 collections were examined from the provinces of Jujuy, Salta, and Tucumán. This subspecies has a well-defined

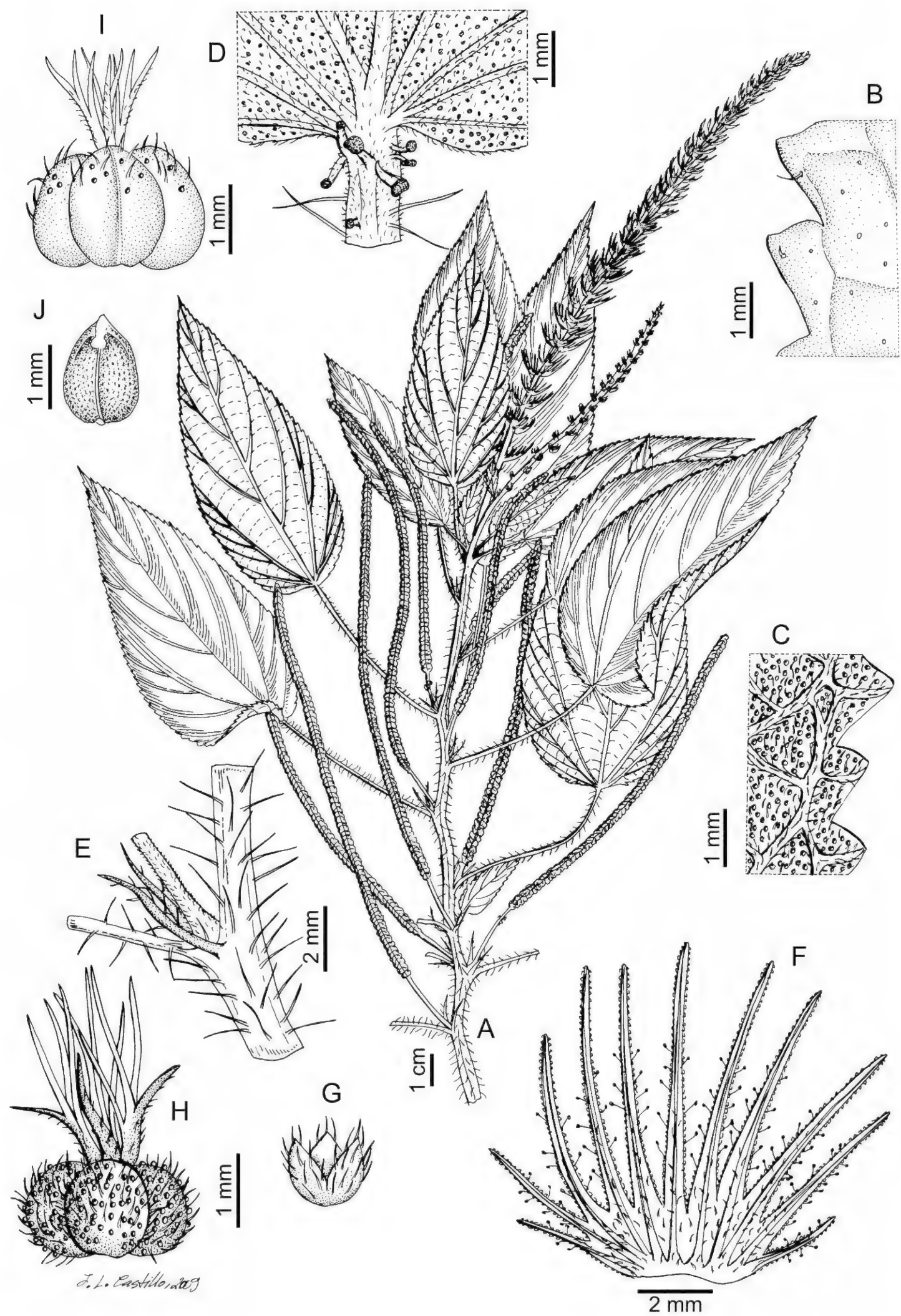


Figure 3. *Acalypha communis* subsp. *apicalis* (N. E. Br.) Cardiel & P. Muñoz. —A. Flowering branch. —B. Detail of upper leaf surface. —C. Detail of lower leaf surface. —D. Detail of leaf blade base, showing resinous droplets, stipels, and trichomes. —E. Detail of node and stipules. —F. Mature bract associated with pistillate flower. —G. Calyx of pistillate flower. —H. Ovary and styles. —I. Capsule and styles. —J. Seed. A–J illustrated from *J. C. Solomon et al. 6911* (MO).

distribution along the north-central Wet Andes region, associated with the Tucumano-Boliviano forest, and has been collected from elevations of (500–)800–1400(–2000) m (Fig. 1E).

References. Cardiel et al. (2013a, 2013b).

Notes. *Acalypha friesii* was described based on a single collection, *R. E. Fries 178*, of which we have found three duplicates in the S and K herbaria. Since no holotype was designated, we chose the best preserved specimen as lectotype. *Acalypha friesii* was accepted by Lourteig (1954) who located it very close to *A. communis*. After a careful study of the deficient and immature type specimens, we consider that *A. friesii* is conspecific with *A. communis* subsp. *saltensis*. This is the single subspecies of *A. communis* found in Jujuy Province. The differences in the pistillate bracts and ovary pointed out by Lourteig (1954) referred to immature organs.

Acalypha communis subsp. *saltensis* has leaf blades similar in size and shape to those of *A. communis* subsp. *apicalis*, but they are thinly membranaceous, with petioles 6–8(–14) cm long in the former and subchartaceous, with petioles 5(–10) cm long in the latter. The known distributional area of the two subspecies is also clearly differentiated (see Fig. 1C, E).

Selected specimens examined. ARGENTINA. **Jujuy:** Dpto. Santa Bárbara, NE of Libertador, 850 m, 24 Mar. 1994, *C. M. Taylor 11491* (MO). **Salta:** Dpto. Caldera, Mojotoro, 1060 m, 11 Jan. 1941, *T. Meyer 3650* (LIL, NY). **Tucumán:** Dpto. Tafí, orilla de la vía de Tafí a Cadillal, 18 Mar. 1945, *F. Herrera 303* (BM, NY, SI, W).

4e. *Acalypha communis* subsp. *tracheliifolia* (Pax & K. Hoffm.) Cardiel & P. Muñoz, *Taxon* 62: 1300. 2013. Basionym: *Acalypha tracheliifolia* Pax & K. Hoffm. *Pflanzenr.* (Engler) 147, 16(Heft 85): 41. 1924. TYPE: Argentina. Entre Ríos, s.d., *J. Tweedie 62* (neotype, designated by Cardiel et al., 2013a: 1300, BM 999630!).

Iconography. Unknown.

Distribution. *Acalypha communis* subsp. *tracheliifolia* is known from northeastern Argentina and Uruguay. In Argentina, four collections were examined from the province of Entre Ríos. In Uruguay, 18 collections were examined from the departments of Canelones, Cerro Largo, Florida, Montevideo, Paysandú, Rocha, Salto, Soriano, and Tacuarembó. This subspecies extends into the Pampas region and has been collected from elevations of 0–200 m (Fig. 1F).

Reference. Cardiel et al. (2013a).

Note. See the notes to *Acalypha communis* subsp. *paraguaruensis*.

Selected specimens examined. ARGENTINA. **Entre Ríos:** Dpto. Uruguay, Banco Pelay, 19 Dec. 1991, *N. M. Bacigalupo & E. R. Guaglianone 1579* (MO). URUGUAY. **Canelones:** Paso Cuello, Río Santa Lucía, 17 Dec. 1935, *B. Rossengurt B 1422* (F). **Cerro Largo:** Río Negro, Palleros, Dec. 1935, *Gallinal et al. B-1421* (GH). **Florida:** Estancia Rincón Santa Elena, Picada Castro, Arroyo Mansavillagra, Dec. 1946, *B. Rossengurt 5845* (MA, MO). **Montevideo:** Monte Video, 1826–1830, *J. Anderson 216* (BM, W). **Paysandú:** Arroyo Negro, 12 Nov. 1937, *B. Rossengurt 2280* (GH). **Rocha:** Arroyo La Pantanosa, 5 Feb. 1938, *B. Rossengurt 2451* (GH). **Salto:** Río Arapey y Arroyo Valentín, 28 Jan. 1937, *B. Rossengurt 980* (F, GH). **Soriano:** Juan Jackson, Dec. 1935, *B. Rossengurt 1420* (F). **Tacuarembó:** Valle Edén, 3 Feb. 1947, *B. Rossengurt 5002* (MA, MO).

5. *Acalypha gracilis* Spreng., *Syst. Veg.* 4(2): 315. 1827. *Ricinocarpus gracilis* (Spreng.) Kuntze, *Revis. Gen. Pl.* 2: 618. 1891. TYPE: Brazil. s. loc., s.d., *F. Sellow [Sello] s.n.* (neotype, designated here, W-167581!; isoneotype, B†, W!).

Iconography. Lourteig and O'Donnell (1942: 316, fig. 12; 1943: tab. 94b); Bacigalupo (2005: 174, fig. 84).

Distribution. *Acalypha gracilis* is known from Brazil (Cardiel, 2010), Argentina, Paraguay, and Uruguay. In Argentina, 36 collections were examined from the provinces of Buenos Aires, Corrientes, Entre Ríos, and Misiones. In Paraguay, eight collections were examined from the departments of Alto Paraná, Caazapá, Guairá, and Itapúa. In Uruguay, four collections were examined from the departments of Artigas, Paysandú, and Salto. *Acalypha gracilis* extends into the Atlantic Forest and Pampas regions, usually in riverside locales, and has been collected from elevations of 100–500 m (Fig. 2A).

References. Bacigalupo (2005), Berry et al. (2007).

Notes. *Acalypha gracilis* was first described by Sprengel, based on a Brazilian specimen collected by Friedrich Sello (or Sellow, as he changed his name in 1814 when he went to Brazil) from “Rio grande,” but we could not find this specimen and presumed it was destroyed. Sello’s herbarium and types were mostly destroyed in the Berlin herbarium fire of 1944. We found several of Sello’s collections of this species, without a precise locality, in the K,

P, and W herbaria (some of them were used later to describe other taxa). We selected the most representative specimen for *A. gracilis*, from the W herbarium, as the neotype. The terminal staminate inflorescences of *A. gracilis* are infrequent among the South American species of the genus. In the countries studied herein, this character is also present in *A. herzogiana*, *A. multicaulis*, and *A. striolata* (see differences in the Key to Species).

Selected specimens examined. ARGENTINA. **Buenos Aires:** Punta Lara, Partido de La Plata, 26 Feb. 1946, A. Krapovickas 2887 (F, K, MO, NY). **Corrientes:** Dpto. Alvear, 4 km NE de Alvear, Estancia Santa Ana, 9 Feb. 1979, A. Schinini et al. 16895 (K, NY). **Entre Ríos:** Buenos Aires, 1846, J. Tweedie s.n. (BM). **Misiones:** Loreto, 21 Jan. 1946, J. E. Montes 1783 (GH, K). PARAGUAY. **Alto Paraná:** Monte Grande, 175 m, 13 May 1945, M. S. Bertoni 1344 (NY). **Caazapá:** Parque Nacional Caaguazú, 19 July 1986, L. Molas 729 (F). **Guairá:** Tororo San Pedro, Cerro San Pedro, 15 Dec. 1988, N. Soria 2920 (MA, NY). **Itapúa:** Pirapó, Centro de Desarrollo Forestal, 21 Apr. 1983, R. Duré & L. Pérez 202 (MO). URUGUAY. **Artigas:** Arroyo Itacumbú, 23 Jan. 1942, B. Rosengurt B-3764 (GH). **Paysandú:** Isla del Queguay Grande, Rio Uruguay, May 1938, A. Lombardo (GH). **Salto:** Isla Gaspar, 14 Dec. 1905, M. B. Berro (K).

6. *Acalypha hassleriana* Chodat, Bull. Herb. Boissier, sér. 2, 5: 606. 1905. TYPE: [Paraguay. Canindeyú]: Yerbales, Sierra de Maracayú, ad ripam fluminis Jejui guazu, Dec., *E. Hassler* 5678 (lectotype, designated by Cardiel et al., 2013a: 1302, P [barcode P00635268]!; isoelectotypes, B not seen, BM!, GH!, K!, NY!, P!, UC!, W!).

Acalypha glandulosa Chodat & Hassl., Bull. Herb. Boissier, sér. 2, 5: 605–606. 1905, nom. illeg., non *Acalypha glandulosa* Cav., Anales Hist. Nat. 2: 141. 1800. *Acalypha hassleriana* var. *glandulosa* (Chodat & Hassl.) Pax & K. Hoffm. Pflanzenr. (Engler) 147, 16(Heft. 85): 41. 1924. TYPE: [Paraguay.] Inter rupes pr. Chololo in valle fluminis Y-aca, Dec., *E. Hassler* 6689 (lectotype, designated by Cardiel et al., 2013a: 1302, P [barcode P00635865]!; isoelectotypes, BM!, K!, NY!, P [2]!, UC!, W!).

Acalypha glandulosa var. *brevistachya* Chodat & Hassl., Bull. Herb. Boissier, sér. 2, 5: 606. 1905. TYPE: [Paraguay.] Inter rupes pr. Chololo in valle fluminis Y-aca, Dec., *E. Hassler* 6689a (lectotype, designated by Cardiel et al., 2013a: 1302, P [barcode P00635269]!; isoelectotypes, NY!, P!, S!, W!).

Iconography. Unknown (see Notes).

Distribution. *Acalypha hassleriana* is endemic to Paraguay; it has been found in the departments of Canindeyú and Cordillera (six collections examined). This species seems to be associated with the Atlantic Forest and Chaco regions and has been collected from elevations of 100–500 m (Fig. 2A).

References. Berry et al. (2007), Cardiel et al. (2013a).

Notes. Lourteig and O'Donnell (1942) cited this species as doubtful from Argentina (Misiones), based on a single immature specimen (Zotta, Steullet & Deautier BA 27/63, BA). In our opinion, this specimen, as well as the illustrations published by Lourteig and O'Donnell (1942: 318, fig. 13; 1943: tab. 92), represent a young plant of *Acalypha communis* s.l. The name *A. hassleriana* var. *genuina* Pax & K. Hoffm. (Pax & Hoffmann, 1924: 41) must be considered invalidly published (Art. 26.2 of ICN, McNeill et al., 2012), based on the non-reiterative epithet of the variety. The few specimens found of this distinctive species were collected between 1845 and 1902, and it has not been found again. Those habitats where plants of *A. hassleriana* were collected have been profoundly transformed by human activity, so we cannot rule out the possibility that the species is now extinct. *Acalypha hassleriana* belongs to *Acalypha* sect. *Communes* (Cardiel et al., 2013a) and can be mainly distinguished by its deeply cordate leaf blades with numerous glandular trichomes.

Selected specimens examined. PARAGUAY. **Canindeyú:** Yerbales, Sierra de Maracayú, Dec., *E. Hassler* 5678 (B, BM, GH, K, MO, NY, W). **Cordillera:** Tobatí, Nov. 1902, K. Fiebrig 837 (GH, K).

7. *Acalypha herzogiana* Pax & K. Hoffm., Meded. Rijks-Herb. 40: 24. 1921. TYPE: [Bolivia. Santa Cruz]: in Walde zwischen Rio Pirai und Rio Cuchi, 450 m, Jan. 1911, T. Herzog 1453 (lectotype, designated by Cardiel et al., 2013b: 159, S S-R-7754!; isoelectotype, B† [B neg. F-5294!], Z!). Figure 4.

Acalypha nitschkeana Pax & K. Hoffm. Pflanzenr. (Engler) 147, 16(Heft 85): 88. 1924, syn. nov. TYPE: [Paraguay. Canindeyú]: Sierra de Maracayú, 1898–1899, *E. Hassler* 5125 (lectotype, designated here, P [barcode P00645401]!; isoelectotypes, B† [B neg. F-5302!], BM!, F!, K!, MO!, NY!, P!).

Iconography. Figure 4 herein.

Distribution. *Acalypha herzogiana* is known from Bolivia (Cardiel et al., 2013b), Brazil (Cardiel, 2010), Argentina, and Paraguay. In Argentina, the species has been found in the province of Misiones. In Paraguay, 62 collections were examined from the departments of Amambay, Boquerón [Nueva Asunción], Caaguazú, Canindeyú, Central, Cordillera, Guairá, Paraguari, and San Pedro. *Acalypha herzogiana* extends into the Atlantic Forest and Chaco regions and has been collected from elevations of 50–400 m (Fig. 2B).

References. Berry et al. (2007), Steinmann and Levin (2011), Cardiel et al. (2013b).

Notes. *Acalypha nitschkeana* was described as based on eight Paraguayan syntypes, including *K. Fiebrig 141* (F!, G!, K!), *E. Hassler 613* (BM!, G!, K!, NY!), *Hassler 613a* (G!, K!), *Hassler 2274* (G!), *Hassler 3206* (BM!, G!, GH!, MA!, NY!, W!), *Hassler 5125* (B†, BM!, F!, K!, MO!, NY!, P!), *Hassler 6059* (G!), and *Hassler 12673* (BM!, F!, GH!, K!, MO!, NY!, US!). We selected the most representative and best preserved of those specimens, *E. Hassler 5125* from the P herbarium, as the lectotype. *Acalypha nitschkeana* was described by Pax and Hoffmann (1924), who placed it very close to *A. herzogiana*, with the latter species published by the same authors three years before. The differences indicated were mainly related to the position of the inflorescences, which can be quite variable. After the study of type specimens of both names and additional collections, we think that *A. nitschkeana* must be treated as a synonym of *A. herzogiana*.

Selected specimens examined. ARGENTINA. **Misiones:** *J. F. Molfino s.n.* (BAF not seen; cf. Lourteig & O'Donell, 1942). PARAGUAY. Alto Paraná, 1885–1895, *E. Hassler 2274* (G, syntype, *Acalypha nitschkeana*). **Amambay:** Parque Nacional Cerro Corá, 400 m, 10 Feb. 1982, *J. Fernández-Casas 6151* (NY). **Boquerón [Nueva Asunción]:** L'Asumption, sur les collines herbenses, 25 Oct. 1875, *B. Balansa 1691* (K). **Caaguazú:** Arroyo Yuquyry, 10 Nov. 1990, *E. Zardini & C. Velázquez 23755* (F). **Canindeyú:** Sierra de Maracayu, 1898–1899, *E. Hassler 5125* (B†, BM, F, K, MO, NY, P, syntype, *A. nitschkeana*). **Central:** ad ripam lacus Ypacarai, 1893–1900, *E. Hassler 3206* (BM, G, GH, K, MA, NY, W, syntype, *A. nitschkeana*); *12673* (BM, F, GH, K, L, MO, NY, US, syntype, *A. nitschkeana*). **Cordillera:** Cerro Zanja Jhú, 30 July 1988, *E. Zardini 6206* (F, MO). **Guairá:** Colonia Independencia, Cerro Propiedad, Dibben, 8 Oct. 1967, *A. Lourteig* (C, NY). **Paraguarí:** in regione lacus Ypacaray, 1913, *E. Hassler 12673* (BM, C, F, GH, K, MO, NY); Cordillera de Altos, 1885–1895, *E. Hassler 613* (BM, G, K, NY); Cerro Santo Tomás, s.d., *E. Hassler 613a* (G, K, syntype, *A. nitschkeana*), 20 Sep. 1902, *K. Fiebrig 141* (G, F, K, syntype, *A. nitschkeana*). **San Pedro:** Distr. Lima, Estancia Carumbé, 24 Nov. 1969, *T. M. Pedersen 9387* (GH, K, NY).

8. *Acalypha lycioides* Pax & K. Hoffm., Meded. Rijks Herb. 40: 24. 1921. TYPE: [Bolivia. Santa Cruz]: Bergwald bei Charagua, 1000 m, Dec. 1910, *T. Herzog 1213* (lectotype, designated by Cardiel et al., 2013b: 161, Z-15838!; isolectotypes, F!, S!, Z-15839!).

Iconography. Lourteig and O'Donell (1942: 320, fig. 14; 1943: tab. 91).

Distribution. *Acalypha lycioides* is known from Peru, Bolivia (Cardiel et al., 2013b), and northwest-

ern Argentina. In Argentina, 38 collections were examined from the provinces of Catamarca, Jujuy, La Rioja, Salta, Santiago del Estero, and Tucumán. The distribution of *A. lycioides* extends into the north-central Wet Andes region, is usually associated with dry forest or shrublands, and has been collected from elevations of (500–)1000–2000 m (Fig. 2B).

References. Berry et al. (2007), Cardiel et al. (2013b).

Note. *Acalypha lycioides* is easily recognizable by its narrowly elliptic to lanceolate, small leaves 4.5(–5) cm long.

Selected specimens examined. ARGENTINA. **Catamarca:** Dpto. Pomán, nearly to Colana, 1550 m, 3 Mar. 1973, *P. Cantino 715* (GH). **Jujuy:** Ledesma, Sierra de Calilagua, 800 m, 11 Oct. 1927, *S. Venturi 5406* (BM, F, GH, K, MO). **La Rioja:** Dpto. General Belgrano, Sierra de Los Llanos, 25 Nov. 1959, *A. T. Hunziker 1428* (CORD, MA). **Salta:** Rosario de Lerma, Campo Quijano, 1600 m, 20 Jan. 1929, *S. Venturi 8116* (K, MO). **Santiago del Estero:** Dpto. Choya, 29 km al W de Villa La Punta, 480 m, 1 Dec. 1995, *R. H. Fortunato & R. Micheli 5189* (K, NY). **Tucumán:** Dpto. Río Chico, Escaba, 600 m, 5 Dec. 1913, *L. Monetti 1629* (NY).

9. *Acalypha multicaulis* Müll. Arg., Linnaea 34: 53. 1865. *Ricinocarpus multicaulis* (Müll. Arg.) Kuntze, Revis. Gen. Pl. 2: 618. 1891. TYPE: [Brasil.] In Brasilia, s.d., *F. Sellow s.n.* (neotype, designated by Cardiel et al., 2013b: 163, K!).

Acalypha multicaulis var. *glabrescens* Pax & K. Hoffm. Pflanzenr. (Engler) 147, 16(Heft 85): 88. 1924. TYPE: Paraguay. Cordillera de los Altos, Feb. 1900, *E. Hassler 3856* (lectotype, designated here, W-2626!; isolectotypes, F!, G!, K!, MA!).

Acalypha multicaulis Chodat & Hassler, Bull. Herb. Boiss. 2, sér. 2, 5: 605. 1905, nom. nud. inval., pro syn., *Acalypha nitschkeana* Pax & K. Hoffm., 1924.

Iconography. Lourteig and O'Donell (1942: 322, fig. 13; 1943: tab. 92a); Bacigalupo (2005: 172, fig. 83).

Distribution. *Acalypha multicaulis* is known from Bolivia (Cardiel et al., 2013b), Brazil (Cardiel, 2010), Argentina, Paraguay, and Uruguay. In Argentina, this species has been found in the provinces of Buenos Aires, Chaco, Córdoba, Corrientes, Entre Ríos, Jujuy, Misiones, and Salta (29 collections examined). In Paraguay, 77 collections were examined from the departments of Alto Paraguay, Alto Paraná, Amambay, Caaguazú, Canindeyú, Central, Concepción, Cordillera, Guairá, Itapúa, Misiones, and Paraguarí. In Uruguay, four collections were examined from the departments of Durazno, Salto, and Treinta y Tres. *Acalypha multicaulis* extends in the Chaco, Pampas, and Atlantic Forest regions and has been collected

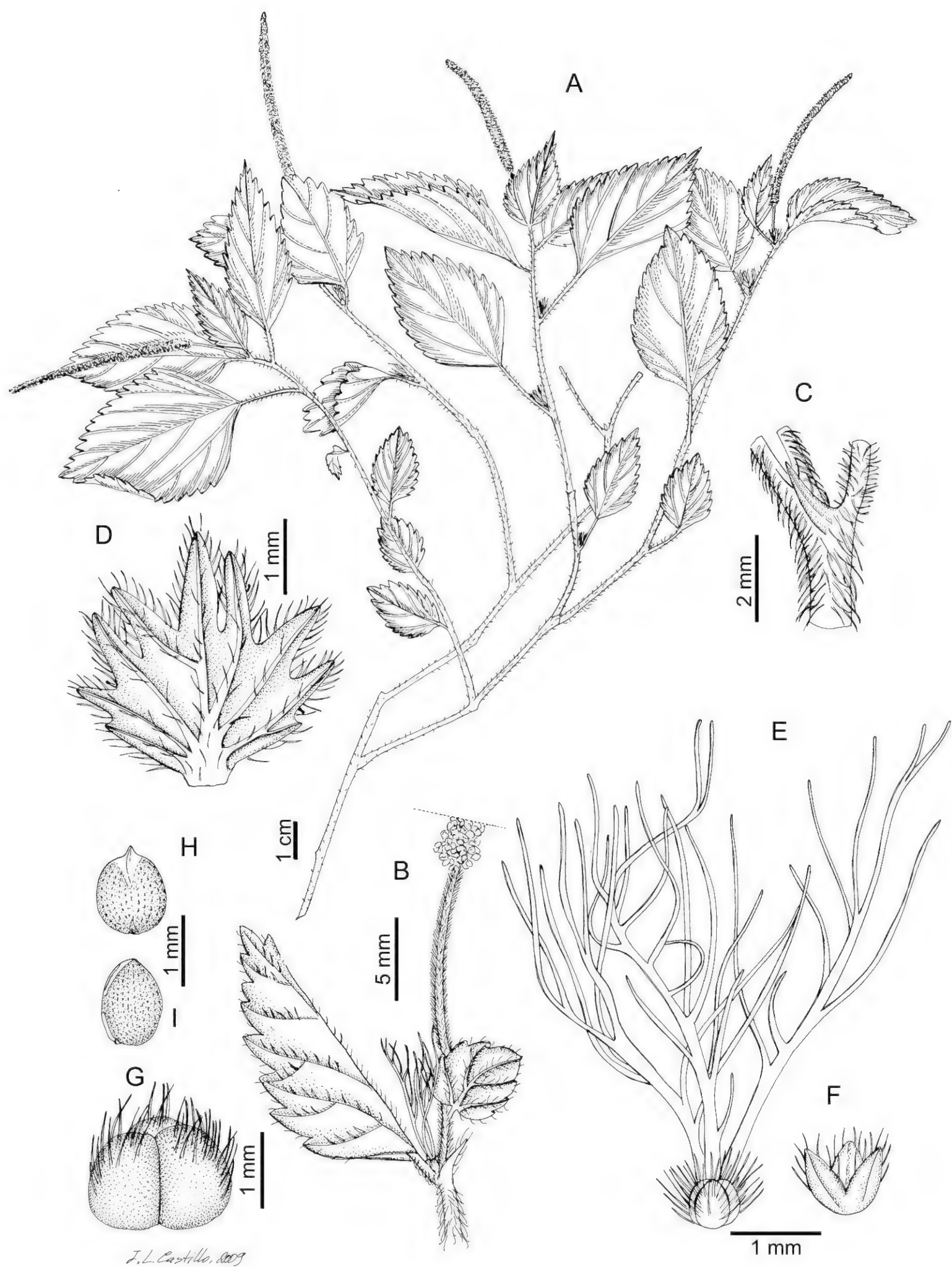


Figure 4. *Acalypha herzogiana* Pax & K. Hoffm. —A. Flowering branch. —B. Detail of branch apex with solitary pistillate flower and base of staminate inflorescence. —C. Detail of node and stipule. —D. Mature bract associated with pistillate flower. —E. Ovary and styles. —F. Calyx of pistillate flower. —G. Capsule. —H, I. Seeds. A–F illustrated from *I. Linneo 900* (MO); G–I from *I. Basualdo 1554* (MA).

from elevations of 0–500 m, notably along riversides (Fig. 2C).

References. Bacigalupo (2005), Berry et al. (2007), Cardiel et al. (2013b).

Notes. *Acalypha multicaulis* var. *glabrescens* was described based on three syntypes, one from Argentina (Misiones, Posadas, s.d., *Muniez 44*, not located) and two from Paraguay (Cordillera de los Altos, *E. Hassler 614*, K!, and *Hassler 3856*, F!, G!, K!, MA!, W!). We selected the better preserved of the known collections, *E. Hassler 3856* from the W herbarium, as the lectotype. *Acalypha multicaulis* is sometimes confused with *A. herzogiana* because of their similar suffruticous habits, terminal staminate inflorescences, and similar leaf shapes. However, *A. multicaulis* has androgynous, mostly staminate inflorescences, with one to several pistillate bracts at the base. In *A. herzogiana*, the inflorescences are usually unisexual.

Selected specimens examined. ARGENTINA. **Buenos Aires:** Lourteig & O'Donnell (1942). **Chaco:** Isla Brasilera, 4 Oct. 1965, A. G. Schulz 15138 (C, F). **Córdoba:** Bacigalupo (2005). **Corrientes:** Isla Apipé Grande, Puerto Arazá, 26 Nov. 1988, S. G. Tressens et al. 3464 (GH, K). **Entre Ríos:** Concordia, Salto Grande, Río Uruguay, Casa de Piedra, 3 Oct. 1978, S. A. Renvoize et al. 2875 (K, MO, NY). **Jujuy:** Bacigalupo (2005). **Misiones:** Salto Iguazú, 160 m, 4 Apr. 1913, Rodríguez 787 (GH, NY, SI). **Salta:** Bacigalupo (2005). PARAGUAY. **Alto Paraná:** Puerto Palma, 1 July 1980, *Itaipú Binacional 800* (MO). **Alto Paraguay:** Puerto Casado, Dec. 1916, T. Rojas 2178 (GH). **Amambay:** 7 km SW of administration of Parque Nacional Cerro Cora, Paso Nande-Jara, 250–300 m, 19 Mar. 1983, J. E. Simonis et al. 126 (MO, NY). **Caaguazú:** Arroyo Yakare'í, 8 Feb. 1989, E. Zardini & M. Velásquez 10774 (F). **Canindeyú:** cerca del Salto del Guairá, Facenda Siete Quedas, 10 Oct. 1980, J. Fernández-Casas & J. Molero 4193 (MA, NY). **Central:** Aregua, 15 Apr. 1945, T. Rojas 12575 (NY, W). **Concepción:** Río Aquidabán, Paso Horqueta, 19 Feb. 1990, R. Palacios 1874 (AS, MO). **Cordillera:** Altos, 19 July 1989, I. Basualdo 2611 (F, MO). **Guairá:** Villa Rica, Oct. 1932, P. Jørgensen 4326 (C, F, GH, NY). **Itapúa:** Hotel Tirul, 6 Apr. 1985, A. Krapovickas & C. L. Cristóbal 40062 (C, F, MO). **Misiones:** Yacutí, Ruta 1, 20 km SE de Santa Rosa, 16 Nov. 1978, M. M. Arbo et al. 1938 (C, F, K). **Paraguarí:** Cordillera de Altos, 1885–1895, *E. Hassler 614* (K, syntype, *Acalypha multicaulis* var. *glabrescens*); Feb. 1900, *E. Hassler 3856* (F, G, K, MA, W, syntype, *A. multicaulis* var. *glabrescens*). URUGUAY. **Durazno:** Rincón de Cabrera, Feb. 1934, C. D. Legrand 329 (F). **Salto:** Isla Redonda, 27 Jan. 1913, M. B. Berro 6453 (K). **Treinta y Tres:** Vergara, 20 m, Dec. 1933, W. G. Herter 91266 (MO).

10. *Acalypha plicata* Müll. Arg. Prodr. [A. P. de Candolle] 15(2): 855. 1866. *Ricinocarpus plicatus* (Müll. Arg.) Kuntze, Revis. Gen. Pl. 2: 618. 1891. TYPE: [Bolivia.] In Bolivia, s.d., T.

Bridges s.n. (holotype, G-DC [barcode G00324504]!; isotypes, BM!, G!, GH!, K!, NY!).

Acalypha cordifolia Hook. f. var. *polyadenia* Griseb., Abh. Königl. Ges. Wiss. Göttingen 24: 60. 1879. TYPE: [Argentina. Salta]: P. G. Lorentz & G. Hieronymus 543 (type, CORD not seen).

Acalypha flabellifera Rusby, Mem. Torrey Bot. Club 6: 119. 1896. TYPE: [Bolivia. Cochabamba]: near snow line, Mt. Tunari, 1891, M. Bang 1109 (lectotype, designated by Cardiel et al., 2013b: 164, NY [barcode NY00246108]!; isoelectotypes, BM!, F!, G!, GH!, K!, MA!, MO!, NY!, US!).

Iconography. Lourteig and O'Donnell (1942: 313, fig. 11; 1943: tab. 90), sub. *Acalypha flabellifera* Rusby.

Distribution. *Acalypha plicata* is known from northern and western South America (Cardiel et al., 2013b) and northern Argentina. In Argentina, 59 collections were examined from the provinces of Catamarca, Jujuy, Salta, and Tucumán. The species distribution extends into the north-central Wet Andes region and has been collected from elevations of (700–)1200–1600 m (Fig. 2C).

References. Berry et al. (2007), Cardiel and Muñoz-Rodríguez (2012), Cardiel et al. (2013b).

Note. *Acalypha plicata* is easily recognizable by its conspicuous glandular trichomes covering young branches, leaves, and inflorescences (see Notes under *A. amblyodonta*).

Selected specimens examined. ARGENTINA. **Catamarca:** Dpto. Ambato, Loc. La Rinconada, 29 Mar. 1995, C. Saravia-Toledo et al. 13159 (GH). **Jujuy:** Dpto. Capital, 6 km N of Jujuy, 1200 m, 2 Oct. 1938, W. J. Eyerdam & A. A. Beetle 22349 (GH, K, MO). **Salta:** Rosario de Lerma, Campo Quijano, 1200 m, 18 Jan. 1941, T. Meyer 3784 (F, LIL, NY). **Tucumán:** Tucumán-Burrucayú, La Ramada F.C.C.A., 450 m, 2 Apr. 1933, A. Peirano s.n. (GH, NY).

11. *Acalypha poiretii* Spreng., Syst. Veg. 3: 879. 1826. *Ricinocarpus poiretii* (Spreng.) Kuntze, Revis. Gen. Pl. 2: 618. 1891. TYPE: “Amer. trop.” s. loc., s.d., *Anonymous s.n.* (holotype, P-LAM [barcode P00382110]!).

Iconography. Lourteig and O'Donnell (1942: 325, fig. 17; 1943: tab. 86).

Distribution. *Acalypha poiretii* is known from the United States, Mexico (Steinmann, 2002), Central America, and the West Indies (Acevedo-Rodríguez & Strong, 2012) as well as Brazil (Cardiel, 2010), Bolivia (Cardiel et al., 2013b), and Argentina. In Argentina, 21 collections were examined from the provinces of

Catamarca, Chaco, Córdoba, Jujuy, La Rioja, Salta, San Luis, Santiago del Estero, and Tucumán. The species is found in the Chaco and north-central Wet Andes regions in foothills and has been collected from elevations of 400–1300 m (Fig. 2D).

References. Berry et al. (2007), Guantay et al. (2008), Cardiel et al. (2013b).

Note. See Notes under *Acalypha boliviensis*.

Selected specimens examined. ARGENTINA. **Catamarca:** Dpto. El Alto, Baleozna, 1250 m, 11 Jan. 1928, *S. Venturi* 7180 (GH). **Chaco:** Las Breñas, 250 m, 16 Feb. 1930, *S. Venturi* 10203 (BM, MO, NY). **Córdoba:** Colón, Ascochinga, 14 Mar. 1944, *C. A. O'Donnell & J. M. Rodríguez* 890 (F, GH). **Jujuy:** Dpto. Santa Bárbara, Vinalito, Yuto, 7 July 1937, *A. L. Cabrera* 4056 (F, NY). **La Rioja:** Dpto. Rosario Vera Peñaloza, Río Totoral, a 5 km de Chelcos, 5 Mar. 1959, *T. A. Hunziker et al.* 14135 (MO). **Salta:** Chicoana, 1200 m, 26 Apr. 1941, *Zabala* 117 (F, NY). **San Luis:** Sierra de San Luis: Bajo de Velis, 26 Jan. 1895, *F. Kurtz* 8496 (NY). **Santiago del Estero:** Guazayán, El Cevilar, 13 Mar. 1944, *S. A. Pierotti s.n.* (BM). **Tucumán:** Dpto. Capital, Villa Luján, 460 m, Jan. 1919, *S. Venturi* 116 (GH, NY).

12. *Acalypha schreiteri* Lillo ex Lourteig & O'Donnell, Lilloa 8: 327. 1942. TYPE: Argentina. Tucumán: Dpto. Tafí, Quebrada de los Saucos, 1800 m, 27 Nov. 1920, *R. Schreiter* 1388 (holotype, LIL-3579!).

Iconography. Lourteig and O'Donnell (1942: 328, fig. 18; 1943: tab. 94a).

Distribution. *Acalypha schreiteri* is endemic to Argentina, known only from the provinces of Jujuy and Tucumán. This species is found in the north-central Wet Andes region and has been collected from elevations of 1500–1800 m (Fig. 2D).

References. Berry et al. (2007).

Note. *Acalypha schreiteri* is a poorly known species. It is mainly characterized by the axillary androgynous inflorescences and the ovate to lanceolate, deeply dentate pistillate bracts, with prominent, lanceolate central teeth.

Selected specimens examined. ARGENTINA. Jujuy: Valle Grande, 28 Feb. 1940, *A. Burkart & Troncoso s.n.* (SI 11557). Tucumán: El Clavillo, 10 Dec. 1916, *P. Jørgensen* 1807 (MO).

13. *Acalypha senilis* Baill., Adansonia 5: 228. 1865. *Ricinocarpus senilis* (Baill.) Kuntze, Revis. Gen. Pl. 2: 618. 1891. TYPE: Uruguay. Banda oriental del Uruguay, cerro das las Animas,

1816–1821, *A. Saint-Hilaire cat. C² n. 2162* (holotype, P [barcode P00645421!]).

Acalypha rotundifolia Herter, Anales Mus. Nac. Montevideo, ser. 2, 1(3): 80. 1911. TYPE: Uruguay. s. loc., s.d., *J. Arechavaleta* 41 (holotype, MVM not seen).

Iconography. None known.

Distribution. *Acalypha senilis* is known from Brazil (Cardiel, 2010), Argentina, Uruguay, and Paraguay. In Argentina, 15 collections were examined from the provinces of Corrientes and Misiones. In Paraguay, three collections were examined from the departments of Amambay and Caaguazú. In Uruguay, four collections were examined from the departments of Maldonado, Montevideo, and Río Negro. In the studied area, the species is found in the Chaco and Pampas regions on sandy soils and has been collected from elevations of 50–200 m (Fig. 2E).

References. Berry et al. (2007), Cardiel et al. (2013b).

Notes. *Acalypha senilis* belongs to *Acalypha* sect. *Communes* (Cardiel et al., 2013a). It is frequently confused with *A. communis* subsp. *communis*. *Acalypha senilis* can be distinguished by its pistillate bracts without glandular trichomes and its ovate to triangular or subrounded leaf blades. *Acalypha communis* subsp. *communis* has pistillate bracts with glandular hairs and ovate to lanceolate leaf blades. In addition, we found some specimens with intermediate characters, so we think that these species could hybridize in the areas where they coexist.

Selected specimens examined. ARGENTINA. **Corrientes:** Dpto. Capital, Localidad Riachuelo, 15 Feb. 1996, *A. Schinini* 30428 (CTES, MA). **Misiones:** Dpto. San Ignacio, Localidad San Ignacio, 19 Nov. 1946, *B. R. Medina* 142 (W). PARAGUAY. **Amambay:** Parque Nacional Cerro Corá, en cerrado próximo al Cerro Muralla, 14 Sep. 1988, *S. Ferruci et al.* 651 (K). **Caaguazú:** entre Yhú y San Blas, 23 Sep. 1980, *J. Fernández-Casas* 3883 (MA, NY). URUGUAY. **Maldonado:** Banda Oriental del Uruguay, Cerro de las Ánimas, 1816–1821, *A. Saint-Hilaire* 2162 (P). **Montevideo:** Montevideo, Fray Peritos, 14 Feb. 1877, *M. Fruchard s.n.* (P [barcode P00645421!]). **Río Negro:** Río Uruguay, July 1867, *E. Gibert* 208 (K).

14. *Acalypha striolata* Lingelsh., Mitth. Thüring. Bot. Vereins, n.s., 29: 48. 1912. TYPE: [Brazil.] “Südbrasilien,” Rio Grande do Sul: Neu-Württemberg, lichter Wald, 450 m., 25 Aug. 1905, *A. Bornmüller* 543 (lectotype, designated here, JE [barcode JE0000819!]; isoelectotypes, G!, HBG!, M!, U!, W!).

Iconography. None known.

Distribution. *Acalypha striolata* is known from Brazil, Argentina, and Paraguay. In Argentina, 21 collections were examined from the provinces of Misiones and Corrientes. In Paraguay, 34 collections were examined from the departments of Alto Paraná, Caazapá, Canindeyú, Guairá, and Itapúa. The distribution of *A. striolata* extends into the Atlantic Forest region, and the species has been collected from elevations of 100–250 m. (Fig. 2F).

Reference. Berry et al. (2007).

Notes. *Acalypha striolata* was described as based on a single Brazilian collection, *A. Bornmüller* 543, of which we have found six duplicates. Since there is no indication of a holotype in the original protologue, nor is there an annotation in this sense by the describing author in the herbarium specimens, we designate the best preserved specimen, from the JE herbarium, as lectotype. *Acalypha striolata* was considered a synonym of *A. gracilis* by Pax and Hoffmann (1924), and this decision was followed by Berry et al. (2007). In our opinion, *A. striolata* is a distinct species, common in southern Brazil, and it is cited here for the first time for Argentina and Paraguay. *Acalypha striolata* differs from *A. gracilis* by its chartaceous leaf blades that are glabrous or nearly glabrous, with the margins usually entire, sometimes obscurely dentate, versus the leaf blades membranous, sparsely pubescent, with dentate margins in *A. gracilis*.

Selected specimens examined. ARGENTINA. **Misiones:** Dpto. San Ignacio, Arroyo Apefru, 15 Aug. 1946, *G. J. Schward* 3167 (LIL, W). **Corrientes:** Dpto. Cainguas, ruta 7.2 km W del acceso a Aristóbulo del Valle, 28 July 1987, *R. Vanni et al.* 774 (K). PARAGUAY. **Alto Paraná:** Km. 200, ruta a Puerto Stroessner, 28 Sep. 1967, *A. G. Schulz* 16204 (C, F). **Caazapá:** camino a la toltería de los Mby'a, 9 Dec. 1989, *N. Soria* 4078 (MA, MO). **Canindeyú:** entre La Paloma y Saltos de Guairá, camino a Puerto Adela, Guazurí, 350 m, 16 Dec. 1982, *J. Fernández-Casas et al.* 7612 (MO, NY). **Guairá:** Colonia Independencia, Cerro Picada, propiedad Dibben, 7 Oct. 1967, *A. Lourteig* 1950 (C, NY, P). **Itapúa:** entre Capitán Meza y Puerto Triunfo, 17 Sep. 1980, *J. Fernández-Casas & J. Molero* 3701 (MA, MO, NY).

15. *Acalypha variabilis* Klotzsch ex Baill., Adansonia 5: 226. 1865. TYPE: Brazil. s. loc., s.d., *F. Sellow* s.n. (lectotype, designated by Cardiel et al., 2013a: 1300, P [barcode P000635221]!; isoelectotypes, B†, P [barcode P000635222]!). Figure 5.

Acalypha hirta Spreng., Syst. Veg. 4 (2, Cur. Post.): 315. 1827, nom. illeg., non *Acalypha hirta* Cav., Anal. Hist. Nat. ii: 141. 1800. *Acalypha communis* var. *hirta* (Spreng.) Müll. Arg., Linnaea 34: 24. 1865. TYPE: [Brazil.] Rio Grande, s.d., *F. Sellow* s.n. (lectotype,

designated by Cardiel et al., 2013a: 1301, W-22068!; isoelectotypes, B, W [2]!).

Acalypha variabilis var. *angustifolia* Baill., Adansonia 5: 227. 1865. TYPE: [Argentina.] Corrientes: s.d., *Dupré* s.n. (holotype, P [barcode P000635226]!).

Acalypha variabilis var. *albescens* Baill., Adansonia 5: 227. 1865. TYPE: Uruguay. s. loc., s.d., *A. Saint-Hilaire* cat. C² n 615 (lectotype, designated by Cardiel et al., 2013a: 1300, NY!).

Acalypha cordobensis Müll. Arg., J. Bot. 12: 228. 1874, as “*cordovensis*.” *Ricinocarpus cordobensis* (Müll. Arg.) Kuntze, Revis. Gen. Pl. 3(3): 291. 1898. TYPE: Argentina. Córdoba: in campo et in Barrancis, s.d., *P. G. Lorentz* 317 (lectotype, designated here, G [barcode G00383634]!; isoelectotypes, CORD!, GOET!).

Acalypha cordobensis var. *rotundata* Griseb., Abh. Königl. Ges. Wiss. Göttingen 24: 59. 1879. *Acalypha communis* var. *rotundata* (Griseb.) Pax & K. Hoffm. Pflanzenr. (Engler) 147, 16(Heft. 85): 40. 1924. TYPE: Argentina. Entre Ríos: Concepción del Uruguay, Oct. 1875, *P. G. Lorentz* 223 (holotype, GOET [barcode GOET006440]!).

Acalypha communis f. *hirsutissima* Chodat & Hassl., Bull. Herb. Boissier, sér. 2, 5: 605. 1905. TYPE: Paraguay. In campo Apepu (flumen Tapiraguay), Aug., *E. Hassler* 4337 (lectotype, designated by Cardiel et al., 2013a: 1301, BM; isoelectotype, P!).

Acalypha montevidensis Klotzsch ex Pax & K. Hoffm. Pflanzenr. (Engler) 147, 16(Heft 85): 39. 1924, nom. nud. inval., pro syn., *Acalypha communis* var. *hirta* Müll. Arg., 1865.

Iconography. Figure 5 herein.

Distribution. *Acalypha variabilis* is known from Bolivia (Cardiel et al., 2013b), Brazil, Argentina, and Paraguay. In Argentina, 98 collections were examined from the provinces of Buenos Aires, Chaco, Córdoba, Corrientes, Entre Ríos, Formosa, Misiones, San Luis, Santa Fe, and Santiago del Estero. In Paraguay, 34 collections were examined from the departments of Amambay, Caaguazú, Cordillera, Misiones, Paraguari, Presidente Hayes, and San Pedro. In Uruguay, 34 collections were examined from the departments of Artigas, Canelones, Colonia, Flores, Lavalleja, Montevideo, Paysandú, Río Negro, Rivera, San José, and Soriano. *Acalypha variabilis* extends into the Chaco and Pampas regions and has been collected from elevations of sea level to 700 m (Fig. 6A).

References. Cardiel et al. (2013a, 2013b).

Notes. *Acalypha variabilis* belongs to *Acalypha* sect. *Communes* Pax & K. Hoffm. (Cardiel et al., 2013a). This species is widely distributed in the studied countries. The species name has been frequently treated as a synonym of *A. communis*, but *A. variabilis* can be mainly distinguished by its pistillate bracts without glandular trichomes and its usually conduplicate leaf blades, with the lower

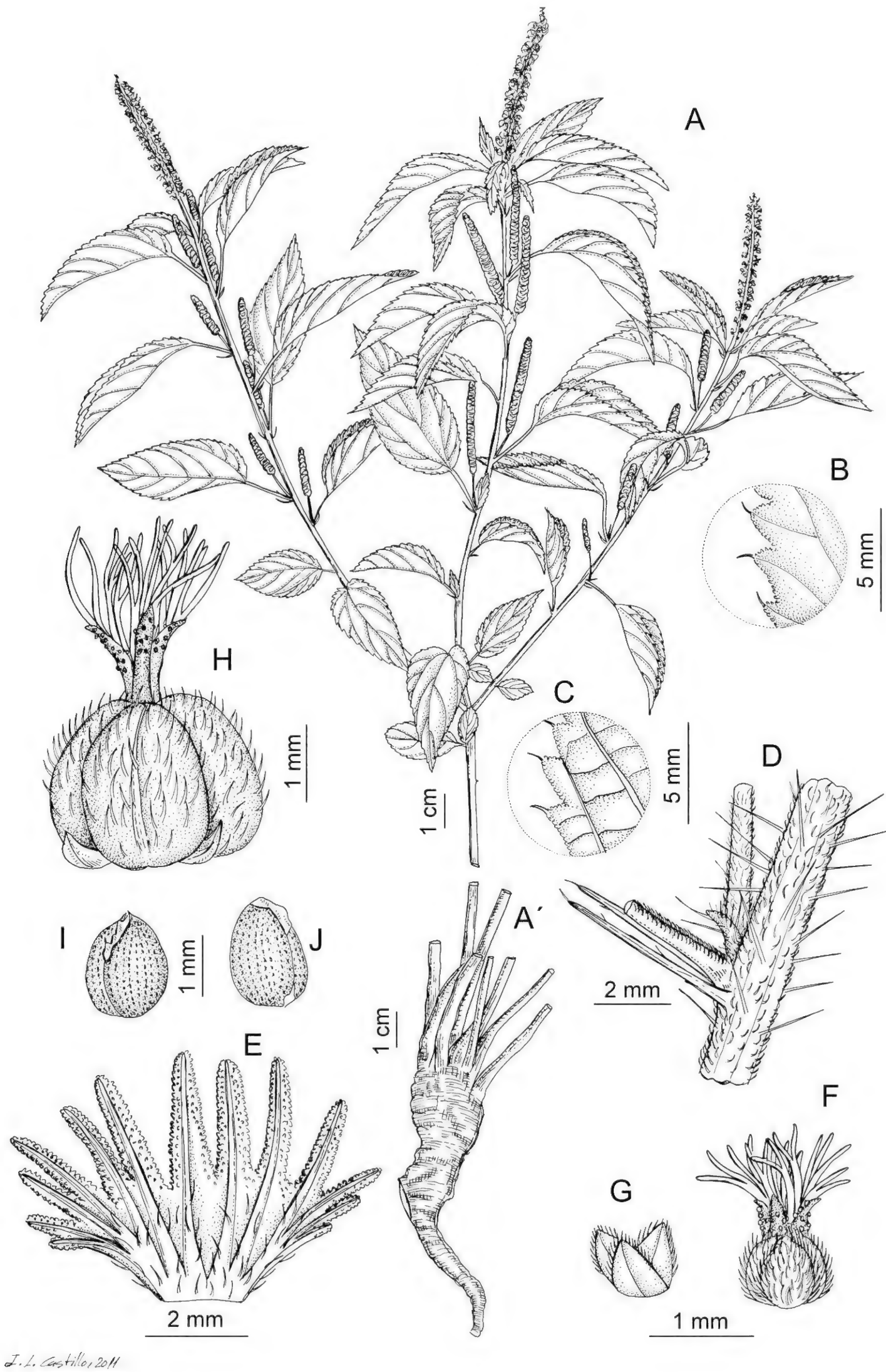


Figure 5. *Acalypha variabilis* Klotzsch ex Baill. —A and A'. Habit. —B. Detail of upper leaf surface. —C. Detail of lower leaf surface. —D. Detail of node and stipules. —E. Mature bract. —F. Ovary and styles. —G. Calyx of pistillate flower. —H. Capsule and styles. —I, J. Seeds. A–D illustrated from *E. Hassler 2986* (MA); E–J from *T. M. Pedersen 8561* (NY).

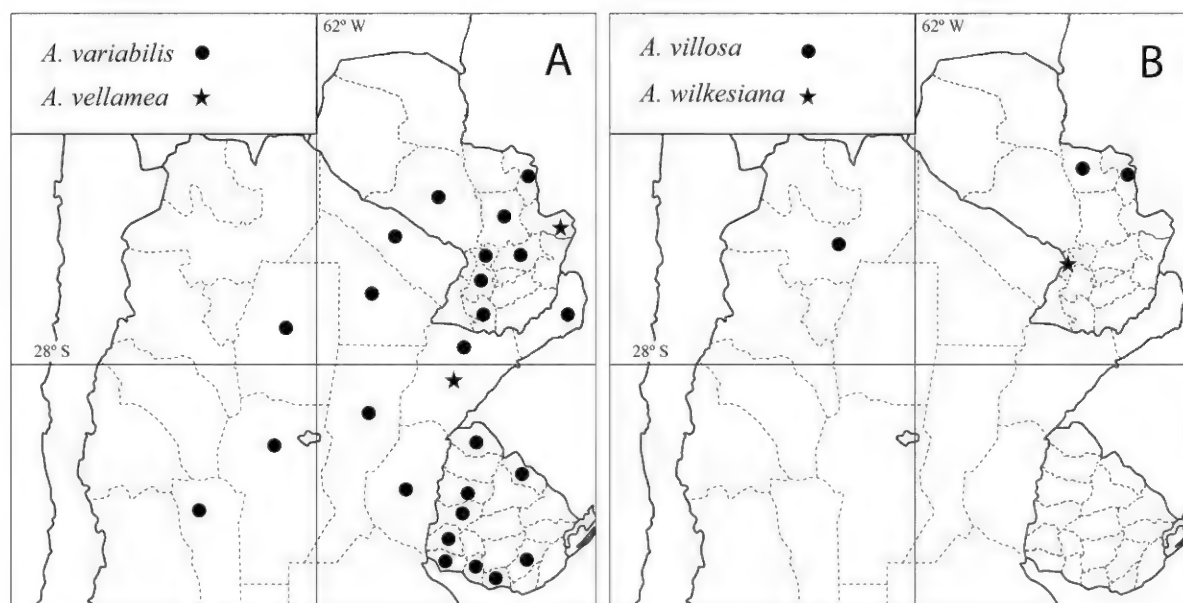


Figure 6. Maps showing distributions in Argentina, Paraguay, and Uruguay of selected *Acalypha* species. —A. *Acalypha variabilis* Klotzsch ex Baill. and *A. vellamea* Baill. —B. *Acalypha villosa* Jacq. and *A. wilkesiana* Müll. Arg.

surface frequently covered by a bright exudate. *Acalypha communis* has pistillate bracts with glandular trichomes and leaf blades that are not conduplicate, without bright exudate.

Selected specimens examined. ARGENTINA. **Buenos Aires:** Flora de la Isla Martín García, Río de La Plata, Oct. 1934, A. L. Cabrera 2880 (NY). **Chaco:** Margarita Belen, 29 Nov. 1945, R. M. Aguilar 511 (F, K, NY). **Córdoba:** La Falda, Cerro El Chorrillo, 950 m, Jan. 1936, M. M. Job 442 (F, GH). **Corrientes:** Dpto. Ituzaingó, Frente a Saltos del Apipé, 21 Nov. 1973, A. Lourteig et al. 2937 (K, NY). **Entre Ríos:** Dpto. La Paz, Piedras Blancas, June–July 1967, T. M. Pedersen 8272 (C, GH, K). **Formosa:** Estancia El Ombú, 19 Dec. 2004, H. Maturo & D. Prado 271 (BM). **Misiones:** Ituzaingó, 8 Oct. 1949, G. J. Schwarz 8170 (NY). **San Luis:** Dpto. Junín, Merlo, Piedra Blanca, 1000 m, 5 Feb. 1947, Diglio-Grassi 2064 (W). **Santa Fe:** Dpto. Las Colonias, Esperanza, 15 Nov. 1946, A. M. R. Huidobro 3257 (C, K, W). **Santiago del Estero:** Sierra de Sumampa, Dpto. Ojo de Agua, Villa Ojo de Agua, 520 m, 10 Feb. 2008, C. Aedo 15282 (MA). PARAGUAY. **Amambay:** Cerro Guazú versus Capitán Bado, Km. 13–15, 16 Dec. 1978, M. Bernardi 19245 (NY). **Caaguazú:** Arroyo Cambay, cerrado scrub, 10 Nov. 1990, E. Zardini & U. Velázquez 23811 (F). **Cordillera:** Emboscada, 4 Apr. 1990, N. Soria 4199 (FCQ, MA). **Misiones:** 12 km W de San Ignacio, camino a Pilar, 15 Nov. 1978, M. M. Arbo 1898 (C, MO). **Paraguarí:** Cordillera de Altos, Jan. 1900, E. Hassler 2986 (BM, F, GH, K, MA, NY, W). **Presidente Hayes:** Gran Chaco, Santa Elisa, 5 Oct. 1905, E. Hassler 2645 (BM, F, GH, K, NY, W). **San Pedro:** Distr. Lima, Estanca Carumbé, 8 Oct. 1967, T. M. Pedersen 8561 (C, K, NY, S). URUGUAY. **Artigas:** Santa Rosa de Cuareim, 50–100 m, Nov. 1927, W. G. Herter 983 (F, GH, NY). **Canelones:** Santa Lucía, 20 Jan. 1938, B. Rosengurt B2409 (F, GH). **Colonia:** Cerros de San Juan, 21 Jan. 1977, T. M. Pedersen 11604 (GH, MO). **Flores:** Río Yí y Arroyo Marincho, 25 Dec. 1936, B. Rosengurt B644 (F, GH). **Lavalleja:** Cerro Arequita, 3 Apr. 1949, B. Rosengurt B-5709 (MA). **Montevideo:** Montevideo, Arechavaleta s.n. (W [7144]). **Paysandú:** Arroyo San Francisco, May 1938, A. Lombardo 3347 (GH). **Río Negro:** Orillas del río Uruguay, Rincón de las Gallinas, Arroyo de los Patos, Estancia de Goneaga, 22–

23 Oct. 1942, B. Rosengurt B-4106 (GH). **Rivera:** Cuñapirú, 600–700 m, 1928, D. Wright s.n. (W). **San José:** Rincón del Pino, ca. de la costa, 10 Nov. 1970, A. Lourteig 2473 (K). **Soriano:** Arenal Grande, 29 Nov. 1932, A. L. Cabrera 2573 (GH).

16. *Acalypha vellamea* Baill., Adansonia 5: 228. 1865. *Ricinocarpus vellameus* (Baill.) Kuntze, Revis. Gen. Pl. 2: 618. 1891. TYPE: [Brazil.] Matto-Grosso: s.d., C. Gaudichaud 246 (holotype, P [barcode P000645427!]).

Acalypha communis var. *brevipetiolata* Chodat & Hassl., Bull. Herb. Boissier, sér. 2, 5: 605. 1905. TYPE: [Paraguay.] In campo in regione cursus superioris fluminis Apa, Dec., E. Hassler 8313 (lectotype, designated by Cardiel et al., 2013a: 1301, BM!; isolectotype, NY!).

Iconography. None known.

Distribution. *Acalypha vellamea* is known from Brazil (Cardiel, 2010), Argentina, and Paraguay. In Argentina, one collection was examined from the province of Corrientes. In Paraguay, two collections were examined, both from the department of Amambay. The species occurs in the Atlantic Forest and Cerrado regions and has been collected from elevations of 300–500 m (Fig. 6A).

References. Berry et al. (2007), Cardiel et al. (2013a).

Notes. *Acalypha vellamea* belongs to *Acalypha* sect. *Communes* (Cardiel et al., 2013a). This is a common species in southern Brazil, but it is scarcely represented in the countries studied herein. The species has been frequently misidentified as *A. communis*, but *A. vellamea* can be mainly distinguished by its young branches and lower leaf surfaces

that are tomentose to velutinous as well as by its subsessile or shortly petiolate leaves. *Acalypha communis* has young branches and lower leaf surfaces variably pubescent, and the leaves are conspicuously petiolate.

Selected specimens examined. ARGENTINA. **Corrientes:** banks of the Paraná near Corrientes, Apr. 1883, *D. Parodi s.n.* (K). PARAGUAY. **Amambay:** Iter ad Paraguaiam Septemtrionalem, in regione cursus superioris fluminis Apa, Dec. 1901–1902, *E. Hassler 8313* (BM, NY).

- 17. *Acalypha villosa*** Jacq., Enum. Syst. Pl. 32. 1760. *Ricinocarpus villosus* (Jacq.) Kuntze, Revis. Gen. Pl. 2: 618. 1891. *Gymnalypha jacquinii* Griseb., Bonplandia 6: 2. 1858. TYPE: [Colombia. Bolívar]: Habitat Carthagenae in silvis & sepibus, tab. 183, fig. 16 in Jacquin, Select. Stirp. Amer. Hist. 1763 (lectotype, designated by Howard & Bornstein, 1989: 10, tab. 183, fig. 16 [Jacquin, 1763]). EPITYPE: tab. 47 in Jacq., Hort. Bon. Vindob. 3. 1776 (epitype, designated by Cardiel, 1995b: 232, tab. 47 [Jacquin, 1776]).

Iconography. Lourteig and O'Donnell (1942: 330, fig. 19; 1943: tab. 95).

Distribution. *Acalypha villosa* is known from Mexico, the West Indies, Central America, northern and western South America, Brazil, Argentina, and Paraguay (Muñoz-Rodríguez et al., 2014).

In Argentina, two collections were examined from the province of Salta. In Paraguay, seven collections were examined from the departments of Amambay and Concepción. This species occurs in cerrado and the north-central Wet Andes regions, in foothills, and has been collected from elevations of 100–400 m (Fig. 6B).

References. Berry et al. (2007), Cardiel and Muñoz-Rodríguez (2012), Cardiel et al. (2013b), Muñoz-Rodríguez et al. (2014).

Notes. *Acalypha villosa* is the only species in the treated area that is not in the autonymic subgenus. It is assigned to *Acalypha* subg. *Linostachys* on the basis of its pedicellate pistillate flowers, five sepals, and inconspicuous pistillate bracts that do not become foliaceous in the fruit. *Acalypha villosa* is the most widely distributed species of this genus in the New World.

Selected specimens examined. ARGENTINA. **Salta:** Orán, Campamento Y.P.F., Río Pescado, 420 m, 26 Feb. 1943, *T. Meyer 4865* (BM, F, LIL). PARAGUAY. **Amambay:** in regione cursus superioris fluminis Apa, Nov. 1901–1902,

E. Hassler 7859 (BM, F, GH, K, MO, NY, W). **Concepción:** Estancia San Luis de la Sierra, 1 km O, 21 Feb. 1990, *R. Palacios 1898* (MO).

- 18. *Acalypha wilkesiana*** Müll. Arg., Prodr. [A. P. de Candolle] 15(2): 817. 1866. *Ricinocarpus wilkesianus* (Müll. Arg.) Kuntze, Revis. Gen. Pl. 2: 618. 1891. *Acalypha amentacea* Roxb. subsp. *wilkesiana* (Müll. Arg.) Fosberg, Smithsonian Contr. Bot. 45: 10. 1980. TYPE: [Fiji.] In insulis Fidji (U.S. Expl. Exped. under Capt. Wilkes), s.d., *B. C. Seeman 22* (holotype, G-DC!; isotypes, GH!, K [2]!, US [2]!).

Iconography. Pérez-Arbeláez (1990: fig. 289).

Distribution. Native to the Melanesian island of Fiji, *Acalypha wilkesiana* is used as an ornamental plant in gardens throughout the tropics and frequently appears to be naturalized. In Paraguay, two collections were examined from the department of Central. The species has been found in the Chaco region and has been collected from elevations of 50–100 m (Fig. 6B).

Notes. *Acalypha wilkesiana* is easily identifiable by its large and broad leaves, usually variegated from coppery green to red.

Selected specimen examined. PARAGUAY. **Central:** Trinidad, Asunción, Reserva Natural, Aug. 1991, *B. Pérez 1034* (MO).

EXCLUDED NAME

Acalypha punctata D. Parodi, Anales Soc. Ci. Argent. 11: 52. 1881, nom. nud. inval., non *Acalypha punctata* Meisn. ex C. Krauss, Flora 28: 83. 1845.

Acalypha punctata D. Parodi was considered by Pax and Hoffmann (1924) as “pessime descripta, verisimiliter ad *A. communem* pertinent.” It was described from Asunción (Paraguay), but no collection is mentioned and it is an invalid name.

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EVOLUTION OF ANGIOSPERM POLLEN. 3. MONOCOTS¹

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ABSTRACT

Monocots, with ca. 65,000 species in 78 families and 12 orders as classified by the Angiosperm Phylogeny Group (Angiosperm Phylogeny Group III, 2009), have traditionally been known as a distinct assemblage from dicots within angiosperms and are now seen as a lineage that diverged from within the more basal of the angiosperm groupings. In this study, the third in a series analyzing pollen characters across the angiosperms, we illustrate the pollen morphological diversity of monocots and analyze 19 palynological and two ecological characters for 120 taxa in 71 families covering the 12 monocot orders and 16 taxa of nine orders in basal angiosperms. Pollen morphological data from previous works and our investigations were optimized onto a new maximum likelihood tree reconstructed from an existing DNA matrix of Chase et al. (2006) using Fitch parsimony, maximum likelihood, and hierarchical Bayesian analysis. From these analyses we infer evolutionary patterns in palynological characters, assess their systematic value, and investigate two aspects (pollination type and habitat moisture) of their ecological adaptation. The highest levels of pollen variation were shown to exist in the Alismatales and Commelinales, with lower levels seen in the Asparagales, Dasypogonales, and Zingiberales; the most variable characters across the phylogeny were found to be pollen outline in polar view, size, and tectum extent. We infer unambiguous plesiomorphic states for monocots and report significant transitions in character states at various levels within the monocot assemblage. Analyses of correlated evolution reconfirmed the hypothesis of an association between exine reduction (or complete loss) and habitat moisture and found significant correlations between various states of exine loss and habitat for hydrophytic–helophytic plants. The presence or absence of the exine itself was found to be more significantly correlated than individual structures, in terms of association with hydrophytic–helophytic plants. The most rapid rate of state changes in pollen characters, in the evolutionary history of monocots, is estimated to have occurred during the Albian-Turonian stage; our work may provide insights into the identification of enigmatic fossil pollen grains from this geological time.

Key words: Character evolution, correlated evolution, exine stratification, habitat moisture, monocots, pollen morphology, pollination type, systematic significance.

Monocotyledonous plants have been recognized as a distinct group, based principally on the single cotyledon of the seed, since the 18th century (Ray, 1703). Monocots are one of the most distinctive major lineages of angiosperms, with ca. 65,000 known species in 78 families and 12 orders, representing ca. 25% of the total diversity of angiosperms (Angiosperm Phylogeny Group III, 2009; Reveal & Chase, 2011). Cladistic studies based on morphological data have indicated putative synapomorphies for monocots that include an adventitious root system, parallel-

veined leaves, scattered vascular bundles in the shoots, cambium presence, and successive microsporogenesis (Donoghue & Doyle, 1989a, 1989b; Loconte & Stevenson, 1991; Doyle & Donoghue, 1992; Doyle & Endress, 2000). Tomlinson (1995) stated that the uniqueness of the monocot vascular system among seed plants and the lack of homology in organization between the primary vascular systems of monocots and other angiosperms might suggest an independent origin of monocots from other angiosperms. However, Tomlinson's observations are

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inconsistent with other morphological characters and molecular data. Scattered vascular bundles and monocotyledonoid floral features are found elsewhere in angiosperms, among basal lineages (Soltis et al., 2005), and the monocots are now known to nest within angiosperms, closely related to the magnoliids (a clade comprising Canellales, Laurales, Magnoliales, and Piperales), as supported by analyses of several nucleotide sequences (Chase et al., 1993; Soltis et al., 1997; Qiu et al., 1999, 2000, 2005, 2006, 2010). Thus, monocots currently form one of the best supported major clades within angiosperms (Chase, 2004; Chase et al., 2006).

Phylogenetic studies of the monocots have made immense strides over the past 20 years, through increasingly extensive taxon sampling and the application of molecular data from plastid, nuclear, and mitochondrial genomic regions (e.g., Chase et al., 1993, 2006; Duvall et al., 1993a, 1993b, 2006; Bremer, 2000; Davis et al., 2004; Tamura et al., 2004; Givnish et al., 2006, 2010; Graham et al., 2006; Petersen et al., 2006; Li & Zhou, 2007). The most basally branching monocots have been considered, from morphological inference, to be the aquatic alismatids (a clade including all families of Alismatales except Araceae and Tofieldiaceae; Hutchinson, 1934; Cronquist, 1968, 1981; Takhtajan, 1969, 1991; Stebbins, 1974; Thorne, 1976), Dioscoreales (Dahlgren et al., 1985) or Melanthiales (Thorne, 1992a, 1992b). Since some of the first molecular studies of monocots (Chase et al., 1993; Duvall et al., 1993a, 1993b), *Acorus* L. has been inferred as the basalmost branching taxon and sister to all other monocots, a finding that has received support from almost all subsequent DNA-based analyses.

The most recent angiosperm classification provided by the Angiosperm Phylogeny Group III (2009) recognized 12 monocot orders: Acorales, Alismatales, Asparagales, Dioscoreales, Liliales, Pandanales, Petrosaviales, and the commelinid orders Arecales, Commelinales, Dasypogonales (Dasypogonaceae, Angiosperm Phylogeny Group III, 2009, here recognized as an order following Reveal & Chase, 2011), Poales, and Zingiberales. In this scheme, Acorales are the first branch to diverge from the rest of the group, with the Alismatales second, followed by Petrosaviales and Dioscoreales–Pandanales. Liliales are sister to a large clade of all other core monocots (i.e., Asparagales and the commelinid orders). Although this phylogenetic framework for monocots is mostly well supported at the ordinal level by nuclear, plastid, and mitochondrial data (Chase et al., 2006), the relationships among some lineages have remained controversial. For instance, the positions of the

Dasypogonales and Arecales, relative to other commelinids, are ambiguous, and relationships remain unresolved in Zingiberales, in particular the placements of the Heliconiaceae and Musaceae, as well as in the most basal branches of the Poales (e.g., Kress et al., 2001; Davis et al., 2004; Tamura et al., 2004; Givnish et al., 2006, 2010; Graham et al., 2006; Petersen et al., 2006; Barrett et al., 2014).

Pollen can play a key role in studies of angiosperm evolution due to its morphological variability and its potential to fossilize (Jones & Rowe, 1999). Multiple studies have indicated the taxonomic significance of pollen morphology in monocots, including investigations in Alismataceae (Argue, 1974, 1976), Araceae (Grayum, 1992; Weber et al., 1999; Hesse, 2006), Areaceae (Thanikaimoni, 1970; Sowunmi, 1972; Ferguson, 1986; Ferguson & Harley, 1993; Harley & Baker, 2001), Cyperaceae (Van Wichelen et al., 1999; Simpson et al., 2003), Dioscoreales (Caddick et al., 1998), Eriocaulaceae (Thanikaimoni, 1965; de Borges et al., 2009), Liliaceae (Nair & Sharma, 1965; Kosenko, 1999), Smilacaceae (Chen et al., 2006), and Tecophilaeaceae (Simpson, 1985b). Similarities in pollen wall structure provided evidence for a close relationship between Lemnaceae and Araceae (the former treated as a subfamily within the latter in the Angiosperm Phylogeny Group III; Hesse, 2006), supporting the recent molecular results of Barabé et al. (2002) and Cabrera et al. (2003). Distinctive aperture patterns and tectum sculptures have supported the combination of *Heterosmilax* Kunth and *Smilax* L. in the Smilacaceae and the removal of *Rhipogonum* J. R. Forst. & G. Forst. from Smilacaceae (Chen et al., 2006). Pollen characters, such as aperture pattern and spine type, are also consistent with treatment of the Eriocaulaceae at various taxonomic levels (de Borges et al., 2009). Pollen evolution across the monocots was previously summarized in detail by Zavada (1983), who proposed evolutionary trends in pollen aperture and wall structure parallel to those proposed for other angiosperms by Walker (1974, 1976): this suggested similar selective pressures on pollen characters in monocots and other angiosperms. Increases in the number and number of types of apertures in the pollen grains of the Alismatales, Arecidae, and Liliales, and a reduction of the sulcus among many monocot groups, are obvious trends that, however, have not been investigated in a modern phylogenetic context but, so far, only under traditional classification systems such as that of Cronquist (1981).

The monocots are commonly considered to have originated by the Early Cretaceous (146–100 million years ago [Ma]) and diversified into the major extant

lineages during the Late Cretaceous (100–66 Ma), contemporaneously with other basal angiosperm groups (Herendeen & Crane, 1995; Bremer, 2000; Gandolfo et al., 2000; Chaw et al., 2004; Janssen & Bremer, 2004; Bell et al., 2010; Smith et al., 2010). Pollen grains of monocots from the Early Cretaceous, such as *Liliacidites* Couper and other types with a distinct graded reticulum, have long been regarded as evidence of early monocots (Doyle, 1973; Walker & Walker, 1984, 1986). On the other hand, Gandolfo et al. (2000) questioned all Early Cretaceous records of monocots and stated that the earliest unequivocal monocot fossils are from the Turonian. The apparently sparse fossil record of monocots is probably due to this group's fundamentally herbaceous habit and the fact that some monocot pollen is hard to distinguish from the monosulcate pollen of some basal angiosperms (e.g., Magnoliales; Friis et al., 2006). Friis et al. (2004) argued that the earliest proposed unequivocal monocot fossil was *Mayoa portugallica* Friis, Pedersen & Crane, with poly-plicate and inaperturate pollen grains, which was placed in the Araceae (Pothoideae). However, Hofmann and Zetter (2010) suggested that this placement may be incorrect, based on similarities to the far older Triassic spore taxon *Lagenella martinii* (Leschik) Klaus. The incompleteness and insufficiency of the fossil record have limited our understanding of the evolutionary links between extinct and extant taxa and present obstacles to identifying early fossil monocot pollen grains. Therefore, determining plesiomorphic pollen states and pollen evolutionary patterns from extant taxa in a phylogenetic context may provide new insights into the palynological characters of the earliest monocots.

Evidence from phylogenetics has indicated that pollinators played an important role in angiosperm diversification (Johnson, 2006; Armbruster & Muchhala, 2009; Kay & Sargent, 2009). Pollen grains of angiosperms may be transported to the stigma by a variety of biotic and abiotic mechanisms for which pollen structures are adapted (Ackerman, 2000; Dobson & Bergstrom, 2000; Lunau, 2000; cf. Edlund et al., 2004). Relationships have been observed between pollination strategies and pollen features (e.g., Skvarla et al., 1978; Grayum, 1986; Linder, 1998, 2000; Hesse, 2000; Tanaka et al., 2004; Sannier et al., 2009; Wang et al., 2014); pollen wall stratification may be affected by pollination syndrome (reviewed in Hesse, 2000), and reduced exine structures may be associated with hypohydrophily (i.e., underwater cross pollination, Tanaka et al., 2004). Similarly, characteristics such as small grain size appear to be linked to pollen delivery by abiotic

vectors (wind or water; Ackerman, 2000). Aspects of the habitat features (e.g., moisture) have also likely played a substantial role in the evolution of pollen morphology (Ackerman, 2000; Franchi et al., 2002). For instance, “harmomegathy,” a term introduced by Wodehouse (1935) to describe alterations in form that accompany changes in the degree of hydration of pollen grains, allows grains to respond and adapt to their environment. Both aperture closure and pollen-wall folding act to accommodate a decrease in cellular volume due to water loss (Katifori et al., 2010).

The loss or reduction of the exine has been a particularly prevalent and interesting feature of monocots. Pollen grains with a partially or fully reduced exine are typically found in moist environments (such as marshes, swamps, and bogs), where the pollen can remain viable without investing in a protective exine, and especially in the evolution of aquatic groups (Wodehouse, 1935). Exineless or exine-reduced pollen has been found in a large number of monocot families including Araceae (Weber et al., 1998; Hesse et al., 1999; Weber et al., 1999), Asparagaceae and Cannaceae (Erdtman, 1952, 1963; Skvarla & Rowley, 1970; Rowley & Skvarla, 1986), Costaceae (Stone et al., 1981), Cymodoceaceae (Pettitt, 1976, 1981, 1984; Ducker et al., 1978; McConchie et al., 1982; Harris et al., 1994), Haemodoraceae (Simpson, 1989), Heliconiaceae (Kress et al., 1978; Stone et al., 1979; Kress & Stone, 1983), Hydrocharitaceae (Pettitt, 1981; Tanaka et al., 2004), Lowiaceae (Kamelina & Raven, 1997), Marantaceae (Erdtman, 1952; Sharma, 1968; Furness & Rudall, 1999), Melanthiaceae (Takahashi, 1987), Musaceae (Erdtman, 1952; Sharma, 1968), Strelitziaceae (Hesse & Waha, 1983; Kronstedt-Robards & Rowley, 1989; Rowley et al., 1997), Zingiberaceae (Theilade & Theilade, 1996), and Zosteraceae (Pettitt & Jermy, 1975; Pettitt, 1976). Elsewhere in angiosperms, exineless or exine-reduced pollen is almost entirely restricted to basal-branching groups such as Annonaceae (Waha, 1987), Ceratophyllaceae (Takahashi, 1995), Degeneriaceae and Gomortegaceae (Rowley & Vasanthy, 1980; Kubitzki, 1981; Hesse & Kubitzki, 1983; Rowley & Vasanthy, 1993), Hernandiaceae (Rowley & Vasanthy, 1980; Kubitzki, 1981; Hesse & Kubitzki, 1983), and Lauraceae (Rowley & Vasanthy, 1980; Kubitzki, 1981; Hesse & Kubitzki, 1983; Gabarayeva et al., 2010), with an exception being the obligate aquatic species of *Callitriche* L. in Plantaginaceae (Osborn et al., 2001). For a fuller listing of exineless taxa, see Furness and Rudall (1999), and for reviews of aquatic taxa in particular, see Cox (1988), Osborn and Philbrick (1994), Philbrick and Les (1996), and

Cooper et al. (2000). Hesse and Kubitzki (1983) claimed that truly exineless pollen is found only in the seagrass taxa of Alismatales, *Amphibolis* C. Agardh (Cymodoceaceae), *Halophila* Thouars (Hydrocharitaceae), and *Thalassodendron* Hartog (Cymodoceaceae), with other taxa (e.g., *Canna* L., *Heliconia* L., and *Strelitzia* Aiton in Zingiberales) retaining at least vestiges of exine. However, Cooper et al. (2000) stated that fully exineless pollen can also be found in some aquatic species of *Callitriche*.

Exine reduction has been described (Furness & Rudall, 1999) as analogous to aperture formation. Since apertures are defined as an opening or thinning within the exine, exineless pollen grains may be functionally either monoaperturate or omniaperturate (in this case, the single aperture covering the entire surface of the grain). However, exineless taxa exhibit a wide range of developmental pathways, in contrast to the single pathway commonly described for aperture formation, by the deposition of apertural shields of endoplasmic reticulum that block the deposition of sporopollenin. Since exine may be laid down on a fibrillar layer (primexine) within the callose wall during the tetrad period of microsporogenesis, or mediated earlier by the plasma membrane and glycocalyx (Takahashi, 1987), exineless pollen grains may be generated either by a lack of primexine (perhaps as in *Ceratophyllum* L., Ceratophyllaceae, Ceratophyllales [Takahashi, 1995] and partially in *Canna*, Cannaceae, Zingiberales [Skvarla & Rowley, 1970; Rowley & Skvarla, 1986]), callose (perhaps the case in *Callitriche*; Osborn et al., 2001), or exine, or by subsequent loss of exine (e.g., *Zingiber* Mill., Zingiberaceae, Zingiberales; Theilade & Theilade, 1996). However, *Canna* does have primexine in the shape of the spines, which do not become exine. Also, within the primexine of typical pollen grains, sporopollenin only polymerizes at specific sites—the parts of the primexine that do not accumulate sporopollenin are later dispersed—appearing as empty voids in the mature pollen wall, such as the spaces between columellae. Frequently, exine loss is accompanied by some degree of compensation in other layers, such as the retention of the primexine or the thickening and elaboration of the intine (Kress & Stone, 1982; Theilade & Theilade, 1996; Franchi et al., 2002).

The extensive accumulation of pollen morphological data and an increasingly robust phylogenetic framework for angiosperms based on advanced molecular analyses together allow for more reliable reconstruction of morphological character states for extant flowering plants and their evolution in a phylogenetic context (Endress & Doyle, 2009; Wortley et al., 2015). The pollen morphology and evolution of monocots are integral to our understand-

ing of morphological evolution in the angiosperms as a whole. In this paper, we survey variation in pollen characters and infer key character state transitions in various lineages based on the most up-to-date phylogenetic framework, using Fitch parsimony (FP), maximum likelihood (ML), and hierarchical Bayesian inference (HB), in order to reveal pollen evolutionary patterns and trends throughout the monocots and to assess the systematic value of pollen characters as evidence for hitherto uncertain relationships within this group. We also perform correlated evolution analyses between pollen traits and ecological characters, to provide further insights into adaptive evolutionary mechanisms and driving forces for pollen character state changes in monocots, as corroborated with data on divergence times for the lineage from previous works. The integration of pollen data and analysis in this study may also facilitate the interpretation of early fossil monocot pollen grains.

MATERIALS AND METHODS

POLLEN DATA COLLECTION

Pollen grains from 20 species in 20 families covering all 12 orders within monocots were examined by LM and SEM to demonstrate the pollen variability of monocots. Pollen samples were collected from the living collections of the Kunming Botanic Garden (KBG) and Xishuangbanna Tropical Botanical Garden (XTBG), China, and from herbarium specimens of the Kunming Institute of Botany (KUN), China, Royal Botanic Garden Edinburgh (E), U.K., and Australian National Herbarium (CANB; for voucher details see Appendix 1). Anthers from herbarium material for LM and SEM observation were softened in warm water for 5 to 10 minutes and then dehydrated through an ethanol series to 100% ethanol. The acetolysis method was inapplicable because most pollen grains of monocots are fragile and liable to collapse. For SEM, anthers were mounted on specimen stubs with double-sided sticky tape and then carefully dissected to expose the pollen grains. The stubs were sputter-coated with gold. Pollen morphology was examined using a Hitachi (Tokyo, Japan) S-4800 SEM at 10.0 kV (KUN). To dry extremely delicate pollen grains (such as those with a very thin pollen wall) while preserving their surface structure for SEM observation, treatment with 2,2-dimethoxypropane (DMP) and critical-point drying (SPI-DRY Critical Point Dryer, No. 13200-AB Manual CPD; SPI Supplies, West Chester, Pennsylvania, U.S.A.) was performed according to Halbritter (1998). Pollen size (the maximum diameter of a single grain) was measured under LM. Note that, due to our

preparation methods, sizes may not be directly comparable with those in the literature derived from acetolyzed grains.

POLLEN CHARACTERS AND CODING STRATEGY

Pollen data were extracted from the literature (primarily SEM and transmission electron microscopy [TEM] observations), online databases, and new observations presented in this paper (see Appendix 1). Palynological terminology follows that of Punt et al. (2007) and Wortley et al. (2015).

The character selection and coding strategy followed those of Wortley et al. (2015) and Harley and Zavada (2000). For reconstruction of character evolution, 19 pollen characters were selected for coding: dispersal unit, polarity, symmetry (in polar view), basic shape, shape class, outline in polar view (amb), size (diameter of largest axis), aperture number, aperture position, aperture membrane, aperture shape, annulus, exine extent, tectum extent, supratectal element presence/absence, supratectal element shape, tectum sculpture, infratectum structure, and foot layer presence/absence (see Table 1 for coded character states). Two ecological characters, pollination type and habitat moisture, were also coded (see Table 1 for coded character states). Characters were treated as unordered binary or multistate characters, with inapplicable states coded as “-” and unknown data as “?”. We adopted two coding methods, the comprehensive method sensu Wortley et al. (2015), which includes polymorphic states, and the democratic method (coding for the most common state; Bininda-Emonds et al., 1998). We adopted the composite coding strategy (incorporating inapplicable states into a more inclusive multistate character) advocated by Maddison (1993) for dealing with the inapplicable states. Data matrices are presented in Appendices 2 and 3.

For studies of correlated evolution, seven pairs of palynological character states and one pair of ecological character states, selected on the basis of previous hypotheses of correlation (Kress & Stone, 1982; Theilade & Theilade, 1996; Ackerman, 2000; Franchi et al., 2002; Katifori et al., 2010), were coded as binary presence/absence characters (see Part II of Table 1 for coded character states). Correlations were tested between six exine stratification characters: exine, tectum, eutectum (whether the tectum provides an effective seal against water loss), infratectum (presence of alveolar, granular, columellate, or structureless material beneath the tectum and above the foot layer or endexine), columellate infratectum, and granular infratectum, and two ecological characteristics: helo–hydrophytes or hy-

drophytes (hydrophytes are defined as plants adapted to aquatic environments, and helophytes to wet but marshy habitats; McDonald et al., 2002). This data matrix is presented in Appendix 4.

ANALYSES OF CHARACTER EVOLUTION

Of recent phylogenetic investigations focused on monocots (Davis et al., 2004; Tamura et al., 2004; Chase et al., 2006; Givnish et al., 2006, 2010; Graham et al., 2006; Petersen et al., 2006), the seven-gene phylogenetic tree of Chase et al. (2006) provides the most powerful study of relationships across the group to date (Givnish et al., 2010), with the broadest taxonomic coverage across the widest range of genetic loci (nuclear, mitochondrial, and chloroplast regions). The results were highly congruent with those of other recent phylogenetic studies.

To enable comparative studies based on a phylogenetic tree with branch lengths, a tree was generated based on the original DNA matrix of Chase et al. (2006), obtained from Mark Chase, containing 120 taxa in 71 families covering all 12 orders of monocots (following the Angiosperm Phylogeny Group III system) plus 16 outgroups of nine orders of the basal angiosperms, using maximum likelihood (ML) inference in RAxML (Stamatakis, 2006), including a simultaneous bootstrap analysis of 2000 replicates, under the GTRGAMMA model.

Two strategies for optimization of pollen characters were used: (1) analysis of the comprehensive dataset with Fitch parsimony and hierarchical Bayesian inference (abbreviated as CFP and CHB, respectively) and (2) analysis of the democratic dataset with Fitch parsimony, maximum likelihood, and hierarchical Bayesian inference (hereafter abbreviated as DFP, DML, and DHB, respectively). The ML method as implemented in Mesquite does not accept polymorphisms, which were numerous in our comprehensive dataset; therefore, only the democratic matrix was analyzed under ML. Ecological characters were analyzed only under CFP and CHB. A series of CFP analyses were conducted to determine differences in pollen evolutionary pattern on the much-debated alternative topologies within commelinids and Poales (Janssen & Bremer, 2004; Chase et al., 2006; Graham et al., 2006; Petersen et al., 2006; Givnish et al., 2006, 2010; Soltis et al., 2011; Barrett et al., 2012; Davis et al., 2012; see Fig. 1), with the same number of terminals as that of Chase et al. (2006) but in different phylogenetic skeletons as above.

FP and ML (using the Mk-1 model) optimizations were performed in Mesquite 2.75 (Maddison & Maddison, 2011), and HB optimizations using

Table 1. Pollen and ecological characters and their states used in analyses of character optimization and as defined in this study. Part I indicates character states for 19 pollen characters (1–19) and two ecological characters (20 and 21), which are mapped in Figure 7A, B. Part II indicates binary characters of pollen morphology (a1 to a6) and ecology (b1 and b2) that were used in analyses of correlated evolution. Part II is not mapped on Figure 7A, B.

Part I	
1.	Dispersal unit: 0, monad; 1, permanent tetrad (includes pseudomonads)
2.	Polarity: 0, apolar; 1, heteropolar; 2, isopolar (or subisopolar)
3.	Symmetry (in polar view): 0, bilateral; 1, radial; 2, asymmetrical
4.	Basic shape: 0, boat-shaped; 1, globose; 2, filiform
5.	Shape class: 0, oblate; 1, spheroidal; 2, prolate
6.	Outline in polar view (amb), states as defined by Walker & Doyle (1975): 0, circular (longest equatorial axis [LA]/shortest equatorial axis [SEA] = 1); 1, elliptic ($1 < LA/SEA < 1.5$); 2, oblong ($1.5 \leq LA/SEA < 2$); 3, elongate ($LA/SEA \geq 2$)
7.	Size (diameter of longest axis), states as defined by Walker & Doyle (1975): 0, small (10–24 μm); 1, medium (25–49 μm); 2, large (50–99 μm); 3, very large (100–199 μm); 4, gigantic ($> 200 \mu\text{m}$)
8.	Aperture number: 0, zero; 1, one; 2, two; 3, three; 4, more than three
9.	Aperture position: 0, polar: distal; 1, polar: proximal; 2, equatorial; 3, global
10.	Aperture membrane: 0, smooth (without ectexine); 1, sculptured (with numerous ectexine elements but not operculate); 2, with operculum
11.	Aperture shape: 0, colpate (when at the distal or proximal pole of a pollen grain, we usually term it sulcate); 1, porate; 2, zonate; 3, spiral; 4, syncolpate
12.	Annulus: 0, absent; 1, present
13.	Exine extent: 0, none or merely small patches appearing as sculpture (exineless); 1, homogeneous exine (atectate); 2, fully present
14.	Tectum extent: 0, intectate (without a tectum but with sculpturing); 1, semitectate; 2, eutectate
15.	Suprategal elements: 0, absent; 1, present
16.	Suprategal element shape: 0, gemmate; 1, echinate; 2, verrucate
17.	Tectum sculpture: 0, imperforate; 1, perforate (micro- and macro-); 2, reticulate (foveolate); 3, rugulate; 4, striate; 5, fossulate; 6, areolate; 7, cupulate
18.	Infrategal structure: 0, columellate; 1, granulate; 2, intermediate between granulate and columellate. Terminology is taken from Doyle (2005).
19.	Foot layer: 0, absent; 1, present
20.	Pollination type: 0, self-pollination; 1, wind pollination; 2, insect pollination; 3, water pollination; 4, bat pollination; 5, bird pollination; 6, non-flying mammal pollination
21.	Habitat moisture; states as defined by McDonald et al. (2002): 0, xerophytic (adapted to arid and low water availability soils); 1, mesophytic (adapted to soils of moderate moisture content); 2, helophytic (adapted to wet but marshy habitats); 3, hydrophytic (adapted to aquatic environments).
Part II	
a1.	Exine: 0, absent; 1, present
a2.	Tectum: 0, absent; 1, present
a3.	Eutectum: 0, absent; 1, present
a4.	Infrategal: 0, absent; 1, present
a5.	Columellae: 0, absent (all other infrategal types); 1, present
a6.	Granules: 0, absent (all other infrategal types); 1, present
b1.	Helo-hydrophytes: 0, absent (all other habitat types); 1, present (plant adapted to wet and marsh or aquatic habitat)
b2.	Hydrophytes: 0, absent (all other plant types); 1, present (plant adapted to aquatic habitat)

BayesTraits 1.0 (available from <<http://www.evolution.rdg.ac.uk/BayesTraits.html>>). Both CHB and DHB analyses were run in BayesTraits using BayesMultistate with empirically selected, most appropriate settings: a reversible-jump hyperprior model, prior distribution range for uniform seeding distribution (0–10 distribution, 0–20 distribution, or 0–30 distribution depending on the character), rate variations ranging from 5 to 35, a sampling frequency of 300 to 800 generations, a burn-in of 10,000 generations, and a total of 5,000,000 generations.

In the discussion that follows, the state of the most recent common ancestor (MRCA) was presented only for derived states, in contrast to the plesiomorphic states of the monocots. For ML and HB analyses, we took the state with the highest likelihood or probability at each node to represent the state of this node on the phylogeny.

TESTS OF CORRELATED EVOLUTION

BayesDiscrete tests for correlated evolution on 12 pairs of character states from the palynological and

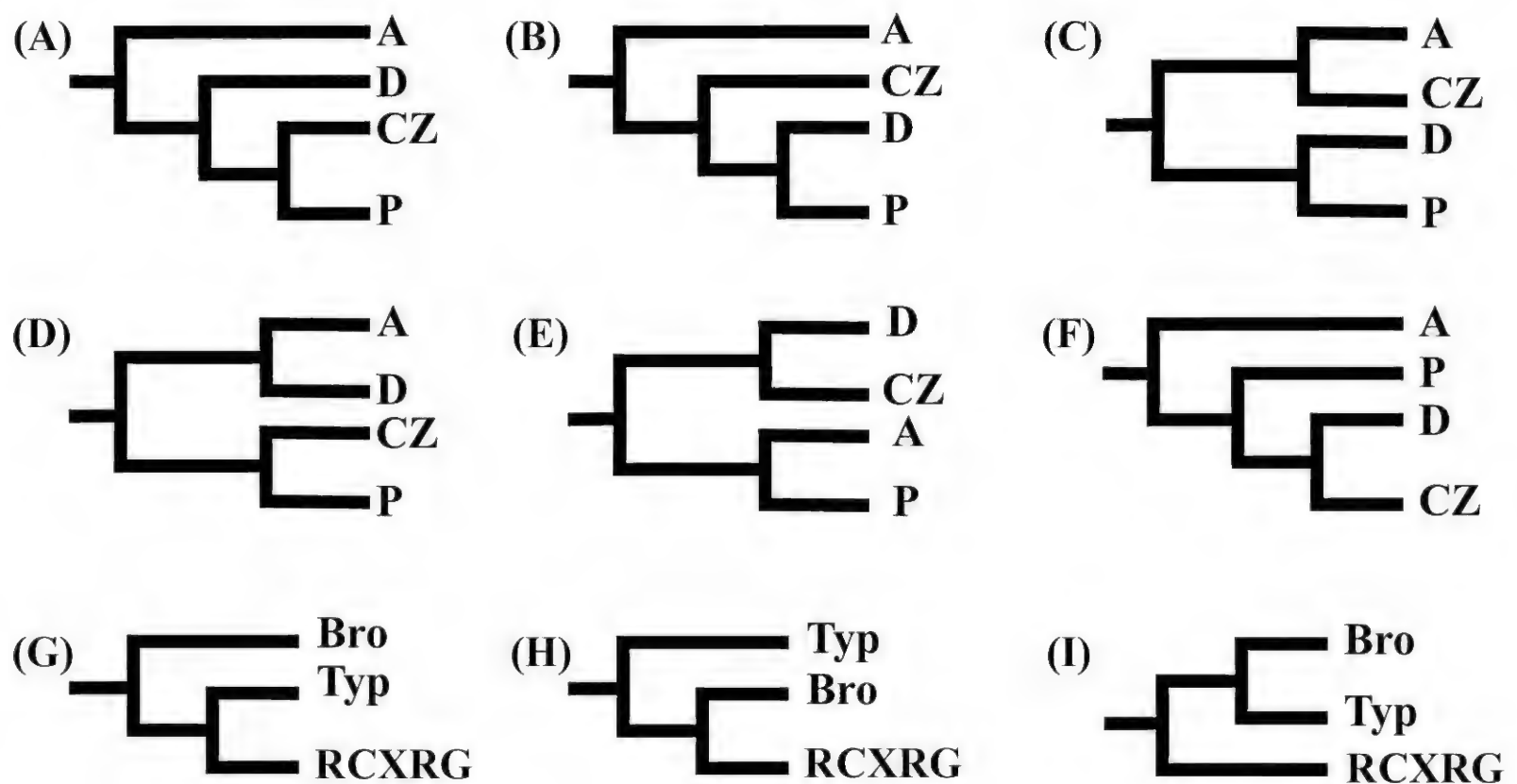


Figure 1. Nine alternative topologies (differing in terms of the internal relationships among commelinids and the basalmost branching group of Poales). A indicates the Arecales; D, Dasypogonales; P, Poales; CZ, Commelinales–Zingiberales; Bro, Bromeliaceae; Typ, Typhaceae; and RCXRG indicates Rapateaceae and the clade comprising the cyperids, xyrids, restiids, and graminids within Poales. The nine topologies correspond to the following recent phylogenetic studies: —A. Janssen & Bremer (2004, p. 390), maximum likelihood (ML) tree in this study. —B. Chase et al. (2006, seven-gene maximum parsimony [MP] tree, pp. 67–68), Peterson et al. (2006, four-gene summarized tree, p. 56, fig. 2A). —C. Chase et al. (2006, four-gene MP tree, pp. 69–70). —D. Givnish et al. (2010, ML tree, p. 592), Barrett et al. (2012, pp. 9, 12), Davis et al. (2012, p. 329). —E. Graham et al. (2006, p. 6), Givnish et al. (2010, MP tree, p. 590). —F. Givnish et al. (2006, p. 39). —G. Chase et al. (2006, seven-gene MP tree, pp. 67–68), Givnish et al. (2010, pp. 590, 592). —H. Graham et al. (2006, p. 6). —I. Chase et al. (2006, four-gene MP tree, pp. 69–70), ML tree in this study, Soltis et al. (2011, p. 7).

ecological data were conducted under ML models (an independent model, I, and a dependent model, D) using the Markov chain Monte Carlo (MCMC) method under the Discrete option in BayesTraits 1.0. A likelihood score representing goodness of fit was calculated for the two models (Table 1, Part II). The likelihood ratio (LR) was determined by $LR = 2$ (likelihood [dependent model]–likelihood [independent model]) and was tested against a χ^2 distribution with four degrees of freedom (following Pagel, 1994). Transition rates for correlated characters were estimated following Pagel and Meade (2006), with eight possible character transitions for each of the six pairs of traits (Fig. 2).

A total of 5,000,000 generations with a burn-in period of 10,000 generations and a sampling frequency of 100 generations was used for both dependent and independent models, using a reversible-jump hyperprior model, exponential prior distribution, and rate variations ranging from 8 to 20. The difference in the harmonic means of the log-likelihoods between the two models was calculated twice. The log Bayes factor value (log BF) was calculated to indicate the degree of evolutionary correlation between two characters: with values of two to five representing a positive correlation, greater

than five a strong correlation, and greater than 10 a very strong correlation (Pagel & Meade, 2006).

We then tested specific hypotheses of contingent evolution by restricting two of the rates to be equal following the method of Pagel (1994) and Schmitt et al. (2009) to test if the loss/gain of a palynological character is related to the absence/presence of an ecological character (Table 1, Part II). The two rate coefficients per trait were created from a model that allows the characters to evolve independently on the tree in the BayesDiscrete tests for correlated evolution. We compared this seven-parameter restricted dependent model to a full dependent model using the likelihood ratio test with one degree of freedom based on Pagel (1994). That is, a significant likelihood ratio would indicate that the parameters were significantly different from one another, demonstrating that the state of one trait influences the direction of evolution of the other. Finally, the exclusiveness of character state changes was tested by restricting one of the rates to zero and recalculating the likelihood ratio of the model. We then compared the restricted seven-parameter model to the unrestricted dependent model using a χ^2 test with one degree of freedom. A significant value would suggest

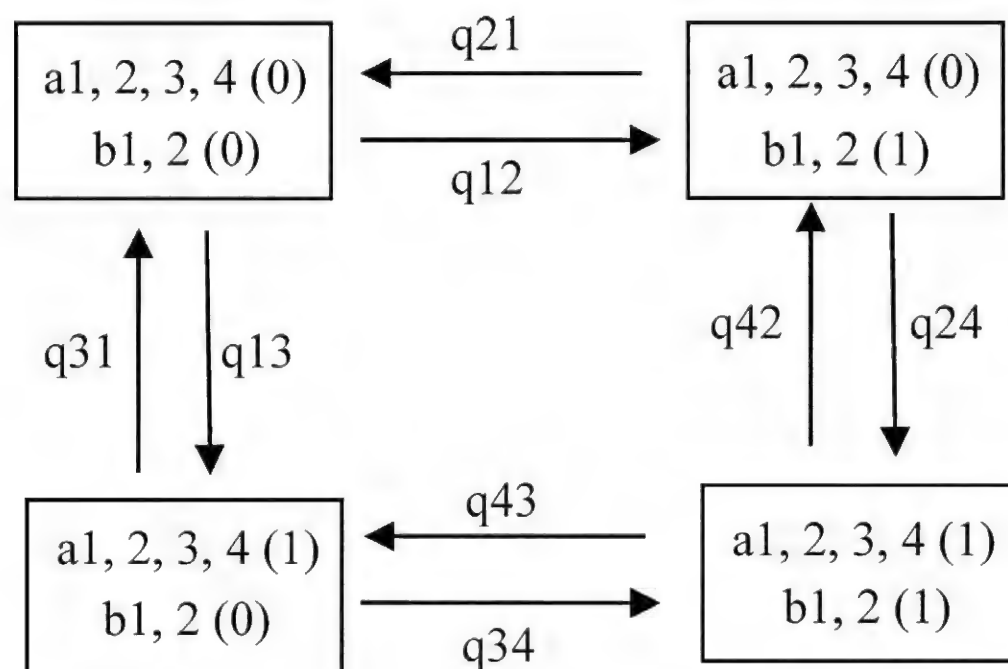


Figure 2. Rate parameters for the eight possible transitions between four pairs of binary pollen characters and binary ecological characters under a model of dependent evolution, exine (character [char.] a1) and helo–hydrophytes (char. b1) or hydrophytes (char. b2), tectum (char. a2) and helo–hydrophytes (char. b1) or hydrophytes (char. b2), eutectum (char. a3) and helo–hydrophytes (char. b1) or hydrophytes (char. b2), infratectum (char. a4) and helo–hydrophytes (char. b1) or hydrophytes (char. b2); characters and states follow Table 1. Arrows indicate direction of transition (only one state transfer while another is stable).

that a character trait was not gained or lost in the presence of another character trait.

Three pollen binary characters, eutectum, columellate infractectum, and granular infractectum, were not analyzed by the contingent evolution test because they were confirmed to be negatively correlated with helo–hydrophyte plants in the BayesDiscrete test.

RESULTS

PALYNOLOGICAL OBSERVATIONS

The pollen morphology of 20 representative taxa observed under LM and SEM is described below to exemplify the diversity of pollen characters and their states in the monocots (Figs. 3–6). The species are presented in phylogenetic order, corresponding to their placement in Figure 7.

Acorus gramineus Sol. ex Aiton (Acoraceae, Acorales, Fig. 3A–C) has pollen dispersed as monads; grains heteropolar, bilaterally symmetrical, boat-shaped, amb usually elliptic; size small (ca. 13–20 μm); monosulcate, aperture distal, with sculptured aperture membrane; tectum with scattered perforations.

Epipremnum pinnatum (L.) Engl. (Araceae, Alismatales, Fig. 3D–F) has pollen dispersed as monads; grains heteropolar, radially symmetrical, globose (spheroidal), amb circular; size medium (ca. 26–30 μm); zonate, aperture equatorial; tectum perforate to fossulate.

Alisma orientale (Sam.) Juz. (Alismataceae, Alismatales, Fig. 3G, H) has pollen dispersed as monads;

grains apolar, asymmetrical, globose (spheroidal), amb circular; size small to medium (ca. 18–22 μm); pantoporate, apertures global, with sculptured aperture membrane; supracteal elements echinate; tectum perforate.

Zostera marina L. (Zosteraceae, Alismatales, Fig. 3I, J) has pollen dispersed as monads; grains apolar, filiform; size gigantic (> 1000 μm long); inaperturate; without exine.

Petrosavia stellaris Becc. (Petrosaviaceae, Petrosaviales, Fig. 3K, L) has pollen dispersed as monads; grains heteropolar, bilaterally symmetrical, boat-shaped, amb elliptic; size small (ca. 16–22 μm); monosulcate, aperture distal; tectum reticulate.

Dioscorea melanophyllum Prain & Burkill (Dioscoreaceae, Dioscoreales, Fig. 4A, B) has pollen dispersed as monads; grains subisopolar, bilaterally symmetrical, globose (oblate), amb elliptic; size small (ca. 14–17 μm); disulcate not situated at a pole, apertures equatorial; tectum fossulate to reticulate.

Stemona tuberosa Lour. (Stemonaceae, Pandanales, Fig. 4C, D) has pollen dispersed as monads; grains heteropolar, bilaterally symmetrical, boat-shaped, amb elliptic; size medium (ca. 26–30 μm); monosulcate, aperture distal; tectum rugulate.

Trillium maculatum Raf. (Melanthiaceae, Liliales, Fig. 4E, F) has pollen dispersed as monads; grains apolar, radially symmetrical, globose (spheroidal), amb circular; size medium (ca. 33–40 μm); inaperturate; tectum rugulate.

Tulipa iliensis Regel (Liliaceae, Liliales, Fig. 4G–I) has pollen dispersed as monads; grains heteropolar,

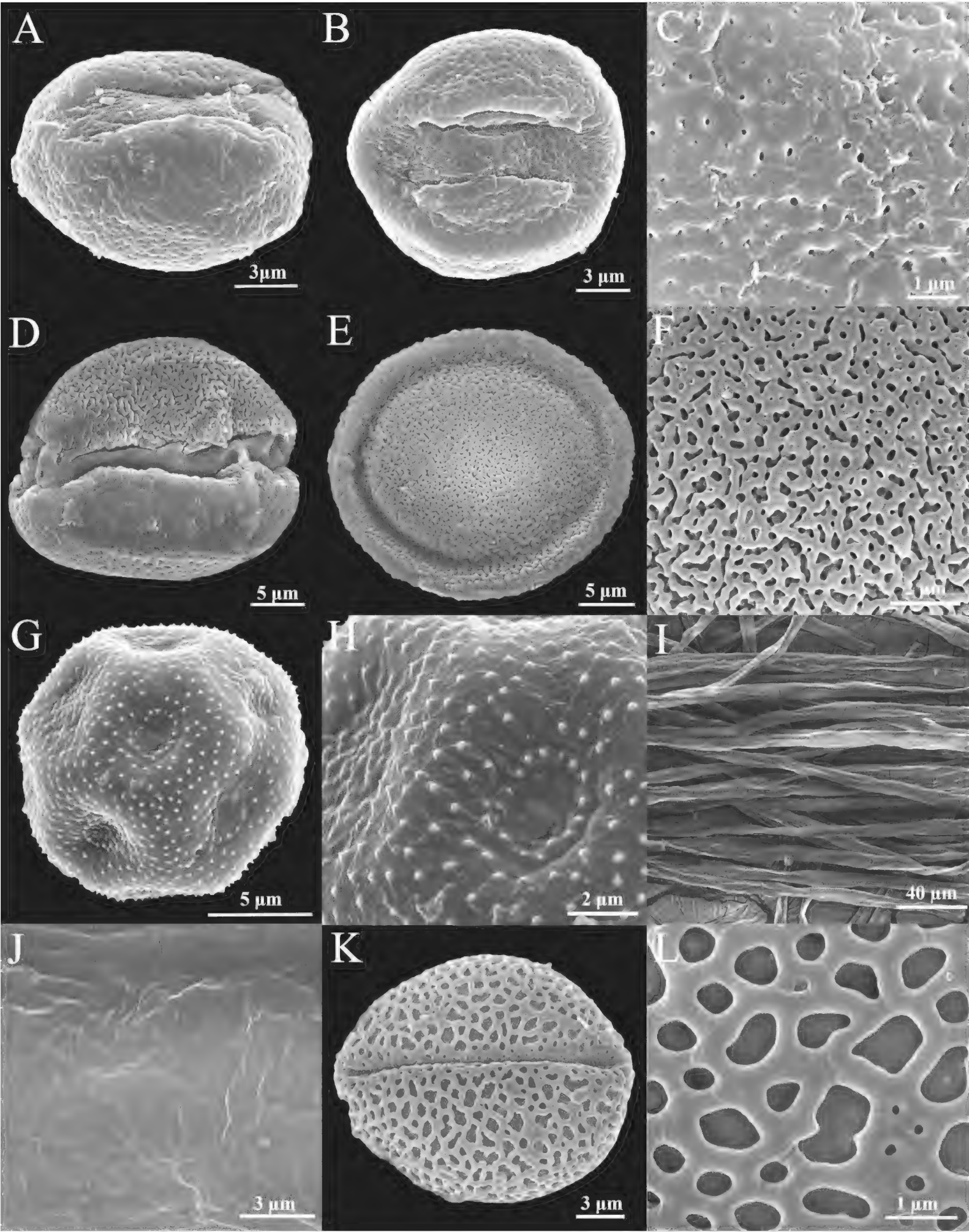


Figure 3. SEMs of monocot pollen, arranged following the topology of Chase et al. (2006). A–C. *Acorus gramineus* Sol. ex Aiton, Acoraceae, Acorales. —A. Equatorial view, showing monad, boat-shaped pollen grain, of small size, with monosulcate aperture. —B. Distal view. —C. Detail of tectum with scattered perforations. D–F. *Epipremnum pinnatum* (L.) Engl., Araceae, Alismatiales. —D. Equatorial view, showing expanded apertural ring (zonate pollen). —E. Polar view. —F. Detail of fossulate to reticulate tectum. G, H. *Alisma orientale* (Sam.) Juz., Alismataceae, Alismatales. —G. Whole grain, pantoporate pollen. —H. Detail of echinate supratectal elements. I, J. *Zostera marina* L., Zosteraceae, Alismatales. —I. Filiform, inaperturate pollen grain. —J. Detail of unsculptured, very thin, and highly reduced exine. K, L. *Petrosavia stellaris* Becc., Petrosaviaceae, Petrosaviales. —K. Polar view, showing boat-shaped pollen grain of small size. —L. Detail of reticulate tectum.

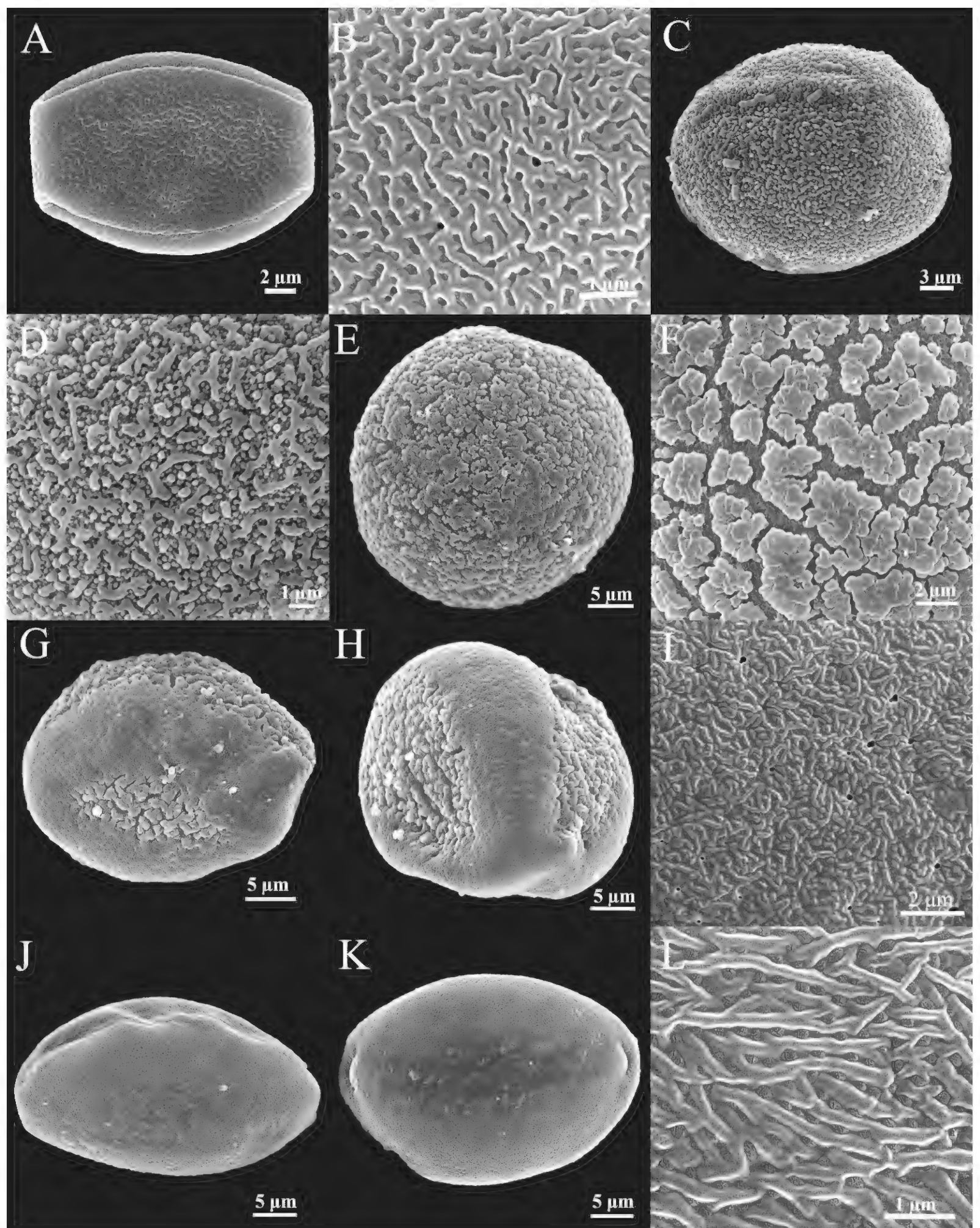


Figure 4. SEMs of monocot pollen, arranged following the topology of Chase et al. (2006). A, B. *Dioscorea melanophyllum* Prain & Burkill, Dioscoraceae, Dioscorales. —A. Polar view, showing disulcate apertures. Note that the pollen grain shown here is rather anomalous; grains of most examples of this taxon are rather more globose. —B. Detail of fossulate to reticulate tectum. C, D. *Stemona tuberosa* Lour., Stemonaceae, Pandanales. —C. Equatorial view, showing monosulcate aperture. —D. Detail of rugulate tectum. E, F. *Trillium maculatum* Raf., Melanthiaceae, Liliales. —E. Spheroidal and inaperturate pollen grain. —F. Detail of rugulate tectum. G–I. *Tulipa iliensis* Regel, Liliaceae, Liliales. —G. Equatorial view, showing colpi located at distal and proximal poles. —H. Oblique equatorial view, showing two colpi located at the proximal pole. —I. Detail of rugulate tectum. J–L. *Allium cyaneum* Regel, Liliaceae, Liliales. —J. Equatorial view, pollen grain of medium size. —K. Distal polar view. —L. Detail of striate tectum.

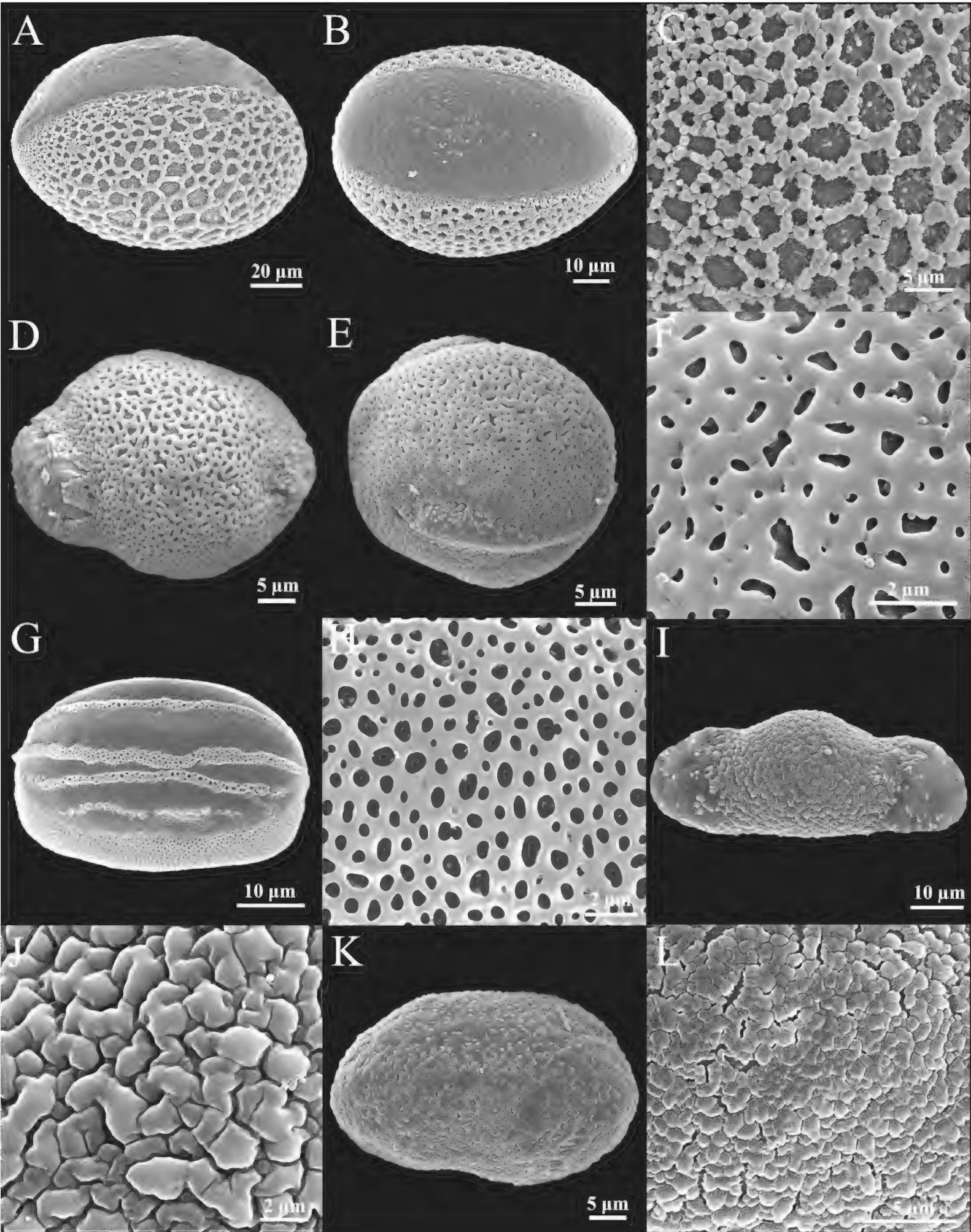


Figure 5. SEMs of monocot pollen, arranged following the topology of Chase et al. (2006). A–C. *Hemerocallis fulva* (L.) L., Xanthorrhoeaceae, Asparagales. —A. Equatorial view, showing very large-size grain. —B. Distal polar view. —C. Detail of reticulate tectum. D–F. *Calamus nambariensis* Becc., Arecaceae, Arecales. —D. Equatorial view. —E. Polar view, showing two equatorially located colpi. —F. Detail of perforate to reticulate tectum. G, H. *Calectasia cyanea* R. Br., Dasypogonaceae, Dasypogonales. —G. Distal polar view, showing monosulcate, operculate aperture. —H. Detail of foveolate tectum. I, J. *Anigozanthos viridis* Endl., Haemodoraceae, Commelinales. —I. Polar view, showing two equatorially located pores. —J. Detail of rugulate tectum. K, L. *Cartonema parviflorum* Hassk., Commelinaceae, Commelinales. —K. Distal polar view, showing sculptured aperture membrane. —L. Detail of areolate to rugulate tectum.

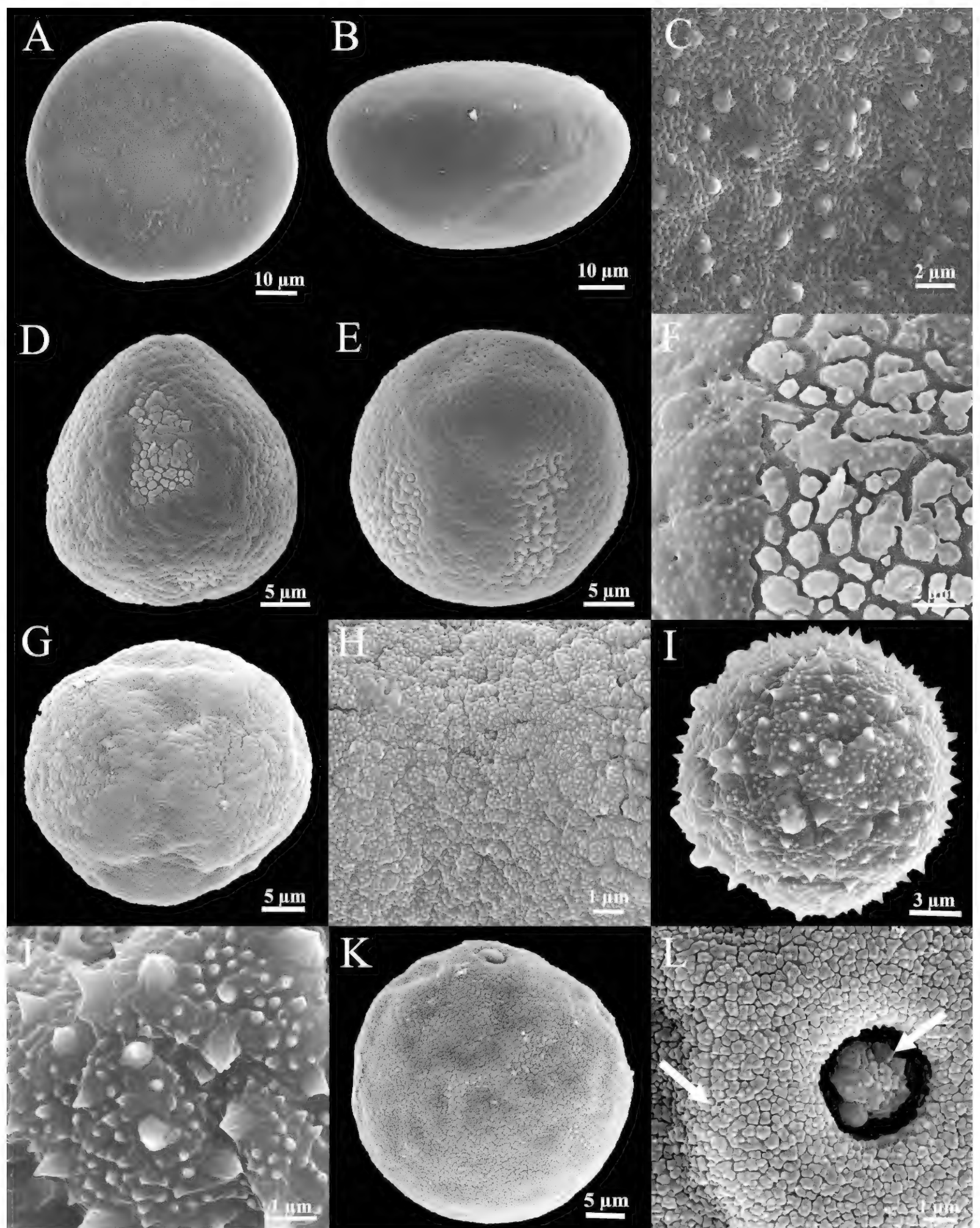


Figure 6. SEMs of monocot pollen, arranged following the topology of Chase et al. (2006). A–C. *Heliconia subulata* Ruiz & Pav., Heliconiaceae, Zingiberales. —A. Distal polar view. —B. Heteropolar, oblate, large, inaperturate pollen grain. —C. Surface of distal polar view, showing granular exinous residues. D–F. *Carex scaposa* C. B. Clarke, Cyperaceae, Poales. —D. Equatorial view, showing single poroid aperture at the distal pole and four to five apertures in the equatorial region. —E. Proximal polar view. —F. Detail of gemmate suprategumental elements. G, H. *Juncus sikkimensis* Hook. f., Juncaceae, Poales. —G. Entire tetrad. —H. Detail of areolate tectum and gemmate suprategumental elements. I, J. *Eriocaulon cristatum* Mart., Eriocaulaceae, Poales. —I. Small, spiral pollen grain. —J. Detail of echinate suprategumental elements. K, L. *Dendrocalamopsis beecheyana* (Munro) Keng f. var. *pubescens* (P. F. Li) Keng f., Poaceae, Poales. —K. Equatorial view, showing single aperture at the distal pole. —L. Detail of areolate tectum; arrows indicate pore with an operculum and annulus.

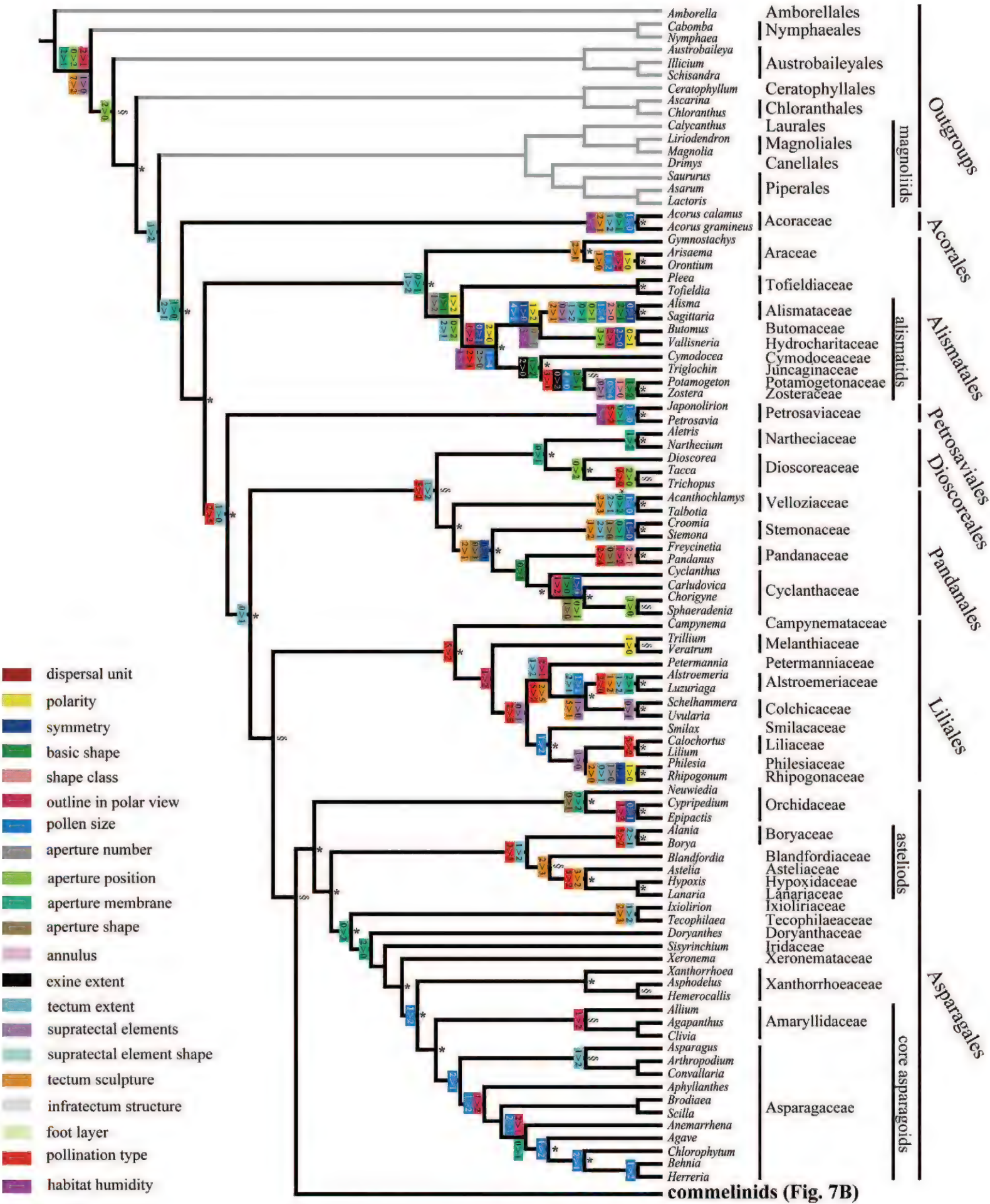


Figure 7. Inferences of character state change for 19 pollen characters and two ecological characters reconstructed with hierarchical Bayesian inference using comprehensive coding on a maximum likelihood phylogeny, based on the molecular data of Chase et al. (2006). Character state changes assume a single transition between differing states at adjacent nodes. Changes on terminal branches are not shown. Numbers on bars indicate the character state transition from the lower to upper node. Character boxes and the number within indicate character state change, following Table 1. §, bootstrap (BP) = 100; *, BP 90%–99%. —A. Seven orders (Acorales, Alismatales, Petrosaviales, Dioscoreales, Pandanales, Liliales, and Asparagales) and outgroups are shown.

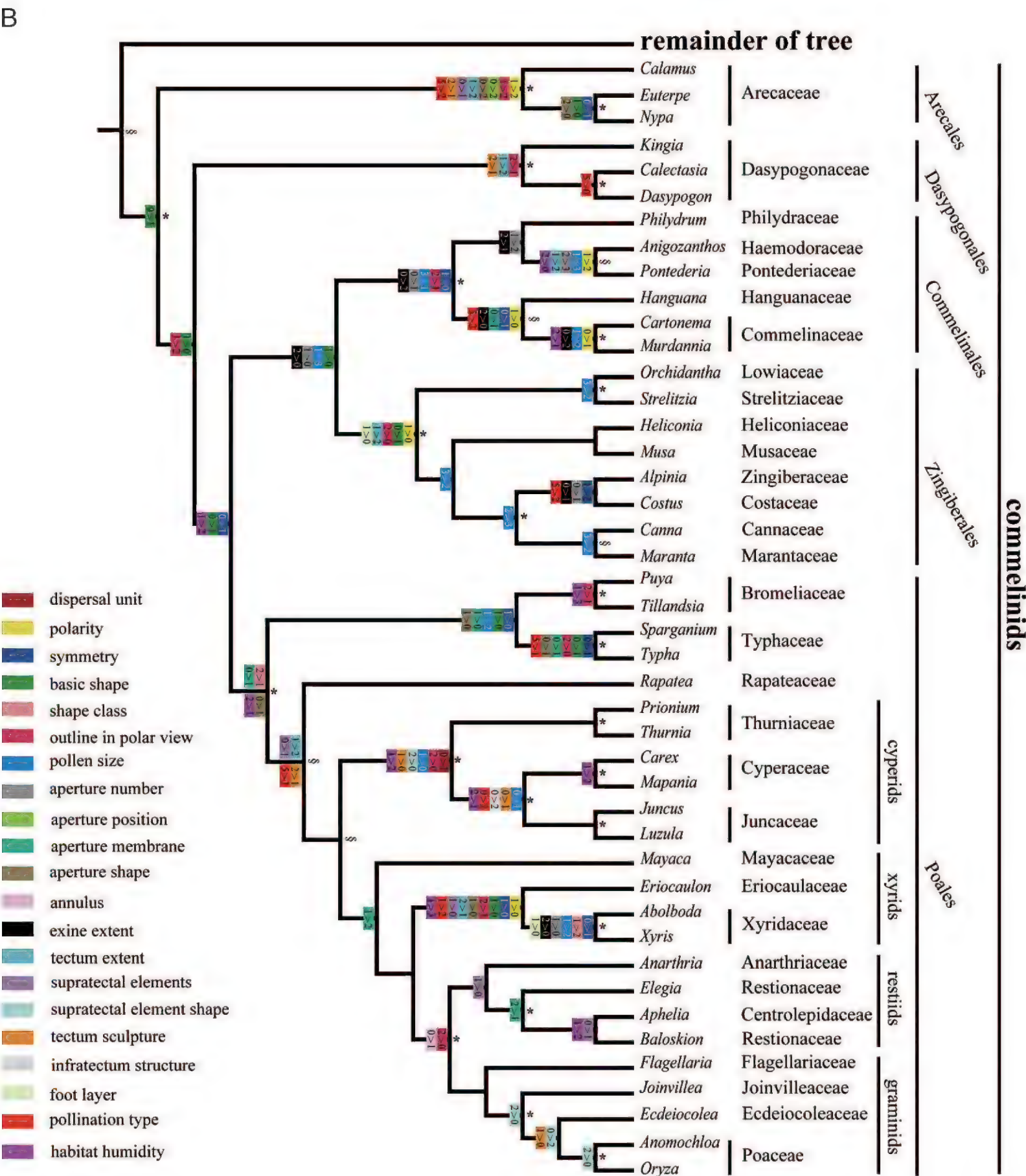


Figure 7. Continued. —B. The commelinid clade is shown.

bilaterally symmetrical, boat-shaped, amb elongate; size medium (ca. 40–45 μm); trisulcate, one aperture distal, two apertures proximal, with sculptured aperture membrane; tectum rugulate.

Allium cyaneum Regel (Amaryllidaceae, Asparagales, Fig. 4J–L) has pollen dispersed as monads; grains heteropolar, bilaterally symmetrical, boat-shaped, amb elliptic; size medium (ca. 28–40 μm); monosulcate, aperture distal; tectum striate.

Hemerocallis fulva (L.) L. (Xanthorrhoeaceae, Asparagales, Fig. 5A–C) has pollen dispersed as monads; grains heteropolar, bilaterally symmetrical, boat-shaped, amb oblong; size large to very large (ca. 85–105 μm); monosulcate, aperture distal; tectum reticulate.

Calamus nambariensis Becc. (Arecaceae, Arecales, Fig. 5D–F) has pollen dispersed as monads; grains heteropolar, bilaterally symmetrical, globose

(spheroidal), amb elliptic; size medium (ca. 30–38 μm); disulcate, aperture equatorial; tectum perforate-reticulate.

Calectasia cyanea R. Br. (Dasypogonaceae, Dasypogonales, Fig. 5G, H) has pollen dispersed as monads; grains heteropolar, bilaterally symmetrical, boat-shaped, amb oblong; size medium to large (ca. 38–56 μm); monosulcate, aperture distal with a unique operculum, not reported elsewhere in angiosperms, comprising a sulcus provided with three elongated, more or less parallel strips of membrane (Chanda & Ghosh, 1976); tectum foveolate-reticulate.

Anigozanthos viridis Endl. (Haemodoraceae, Commelinales, Fig. 5I, J) has pollen dispersed as monads; grains subisopolar, bilaterally symmetrical, globose (oblate), amb elongate; size medium to large (ca. 45–65 μm); diporate, apertures equatorial; tectum rugulate.

Cartonema parviflorum Hassk. (Commelinaceae, Commelinales, Fig. 5K, L) has pollen dispersed as monads; grains heteropolar, bilaterally symmetrical, boat-shaped, amb oblong; size medium (ca. 35–42 μm); monosulcate, aperture distal; tectum areolate to rugulate.

Heliconia subulata Ruiz & Pav. (Heliconiaceae, Zingiberales, Fig. 6A–C) has pollen dispersed as monads; grains heteropolar, radially symmetrical, globose (oblate), amb circular; size large (ca. 64–68 μm); inaperturate; exineless with granulate elements.

Carex scaposa C. B. Clarke (Cyperaceae, Poales, Fig. 6D–F) has pollen grains dispersed as “pseudomonads” (permanent tetrads with three rudimentary grains); grains heteropolar, asymmetrical, globose (prolate), amb circular; size medium (ca. 24–28 μm); polyporate (usually with five or six poroids), apertures distal or equatorial, respectively; supratectal elements gemmate; tectum perforate.

Juncus sikkimensis Hook. f. (Juncaceae, Poales, Fig. 6G, H) has pollen dispersed as tetrads; tetrads radially symmetrical and globose (spheroidal); tetrads of medium size (ca. 34–38 μm); individual grains heteropolar and radially symmetrical, globose (spheroidal), amb circular; monoporate, aperture distal; supratectal elements gemmate; tectum areolate with gemmae and perforations.

Eriocaulon cristatum Mart. (Eriocaulaceae, Poales, Fig. 6I, J) has pollen dispersed as monads; grains apolar, asymmetrical, globose (spheroidal), amb circular; size small (ca. 16–18 μm); aperture spiral; supratectal elements echinate; tectum perforate.

Dendrocalamopsis beecheyana (Munro) Keng f. var. *pubescens* (P. F. Li) Keng f. (Poaceae, Poales, Fig. 6K, L) has pollen dispersed as monads; grains heteropolar, radially symmetrical, globose (spheroidal), amb

circular; size medium (ca. 30–34 μm); monoporate, operculate, with a surrounding annulus, aperture distal; supratectal elements gemmate; tectum areolate.

POLLEN VARIATION

Most of the monocots studied possess heteropolar pollen grains dispersed as monads, with distal monosulcate or monosulcate-derived (e.g., a sulcus reduced to a pore) apertures, and a columellate infratectum, with an exine and foot layer but without an operculum or annulus. In addition to these generally consistent character states, apertural characters in particular show taxonomically ordered patterns of variation: inaperturate pollen predominates in the orders Alismatales and Zingiberales, whereas monosulcate pollen occurs in most taxa within the Liliales and Asparagales, in near-basal lineages such as *Butomus* L. (Butomaceae, Alismatales), in *Gymnostachys* R. Br. and *Orontium* L. (Araceae, Alismatales), and in some genera of Bromeliaceae (Poales). Highly specialized and unique pollen shapes (such as filiform in *Zostera* L.) with a highly reduced exine occur in the seagrass families (Cymodoceaceae, Potamogetonaceae, and Zosteraceae). Pollen morphological variation was observed to exist even within genera (in our comprehensive dataset for monocots, Appendix 2), with especially high variation found in *Dioscorea* L. (Dioscoreales), *Pandanus* Parkinson, and *Stemona* Lour. (both in Pandanales), as well as *Trillium* L. (Liliales), with lower variability seen in *Alisma* L. (Alismatales), *Canna* (Zingiberales), *Juncus* L., and *Typha* L. (both Poales).

ANCESTRAL STATE RECONSTRUCTION

The topology of the new ML tree based on DNA data from Chase et al. (2006) used for character optimization showed some incongruence with the original seven-gene tree derived from maximum parsimony (MP) analysis (Chase et al., 2006). Discrepancies included the positions of Boryaceae, Campynemataceae, Dasypogonaceae, Doryanthaceae, Heliconiaceae, Ixioliriaceae, Mayacaceae, Musaceae, and Typhaceae, for the clade comprising Eriocaulaceae and Xyridaceae, for the position of the genera *Aphelia* R. Br., *Baloskion* Raf., and *Elegia* L., as well as internal relationships within the Asparagaceae s.l., which includes Agavaceae, Aphyllanthaceae, Hyacinthaceae, Laxmanniaceae, Ruscaceae, and Themidaceae (Angiosperm Phylogeny Group III, 2009). Nevertheless, these conflicts were not well supported, with mainly low (bootstrap values below 50%) or

moderate (bootstrap values 50%–80%) support in one or both trees (cf. Fig. 7).

Pollen characters. Of the 19 pollen characters studied, only pollen dispersal unit (cf. Table 1, character [char.] 1) evolved unequivocally throughout all nodes with all five methods. Almost all pollen characters displayed unambiguous plesiomorphic states for monocots as a whole in all five methods (17 characters in analysis of the comprehensive dataset with Fitch parsimony inference [CFP], 19 in analysis of the comprehensive dataset with hierarchical Bayesian inference [CHB], 17 in analysis of the democratic dataset with Fitch parsimony inference [DFP], 19 in analysis of the democratic dataset with maximum likelihood inference [DML], and 18 in analysis of the democratic dataset with hierarchical Bayesian inference [DHB]). The most consistent plesiomorphic states across all five methods were dispersal unit (char. 1) as monad, polarity (char. 2) as heteropolar, pollen size (char. 7) as medium, aperture number (char. 8) as one, aperture membrane (char. 10) as sculptured, aperture shape (char. 11) as colpate, annulus (char. 12) as absent, exine extent (char. 13) as fully present, supratectal elements (char. 15) as absent, infratectum structure (char. 18) as columellate, and foot layer (char. 19) as present. Unambiguous (or probable) plesiomorphic states for the remaining seven characters were not consistently reconstructed across all five methods (char. 5, shape class, and char. 16, supratectal element shape, are inapplicable states for this node). For symmetry in polar view (char. 3), pollen grains were bilateral using CFP, CHB, DML, and DHB, and bilateral or radial under DFP. For basic pollen shape (char. 4), the plesiomorphic state was found to be boat shaped using CHB, DFP, DML, and DHB, and boat shaped or globose under CFP. For outline in polar view (char. 6), pollen grains were found to be circular using DFP and DML, elliptic under CHB, oblong under DHB, and circular or elliptic under CFP. For aperture position (char. 9), a distal position was recovered using DFP, DML, CFP, and CHB, and an equatorial one under DHB; for tectum (char. 14), pollen was semitectate using CFP, DFP, DML, and DHB, and eutectate under CHB. For tectum sculpture (char. 17), pollen was recovered as reticulate using CHB, DFP, DML, and DHB, and perforate or reticulate under CFP.

All 19 pollen characters studied were inferred to exhibit unambiguous state changes on at least one lineage of monocots, using all five analytical methods. The state changes observed at family level or above are summarized in Table 2. Tectum sculpture, aperture membrane, and pollen size for

characters 17, 10, and 7, respectively, had the greatest number of inferred state changes. Pollen dispersal unit (char. 1), annulus (char. 12), infratectum structure (char. 18), and foot layer (char. 19) had the fewest number of changes. Of the 12 orders of monocots investigated, Zingiberales were subtended by the greatest number of state changes (9), Alismatales and Asparagales by the fewest (zero).

Ecological characters. The two ecological characters, pollination type and habitat moisture, were optimized onto the new ML tree using CFP and CHB methods. For pollination type (char. 20), the plesiomorphic state for monocots was found to be wind pollination (under both CFP and CHB). Water pollination was inferred to have evolved on the lineage leading to alismatids (CHB). Herein, alismatids we sampled include the Alismataceae, Butomaceae, Hydrocharitaceae, Cymodoceaceae, Juncaginaceae, Potamogetonaceae, and Zosteraceae (Fig. 7). Shifts to wind pollination occurred in the clade comprising the alismatid families Juncaginaceae, Potamogetonaceae, and Zosteraceae (CHB), in the graminid–restiid clade (CFP), in the Poales excluding Bromeliaceae and Typhaceae (CHB), Typhaceae (CFP, CHB), and Thurniaceae (CFP). Beyond the Poaceae, graminids include the Ectocoleaceae, Joinvilleaceae, and Flagellariaceae; restiids encompass the Anarthriaceae, Centrolepidaceae, and Restionaceae.

For habitat moisture (char. 21), the plesiomorphic state for monocots was inferred as mesic (CFP and CHB). Xeric or drier habitats evolved on the clade comprising Haemodoraceae and Pontederiaceae (CHB). Wetter habitats were found to evolve on six lineages including the clade comprising Commelinales and Zingiberales, and Thurniaceae (Poales; CFP or CHB). Wet habitats evolved on four lineages, i.e., Acorales, core alismatids (Alismatales), Typhaceae (Poales), and the clade comprising Eriocaulaceae and Xyridaceae (CFP and/or CHB; cf. Table 2).

POLLEN CHARACTER STATE CHANGES

The minimum number of state change steps of each of the 19 pollen characters optimizing on the nine alternative topologies tested (Fig. 1) were counted in the CFP analysis. Fifteen characters (excluding symmetry, basic shape, shape class, and outline in polar view [amb]) possessed the same minimum number of steps throughout all nine topologies. Within the topologies, A through F focus on the controversial relationships among major clades within commelinids, and topologies A, D, and E yield the fewest steps for symmetry and basic shape.

Table 2. Pollen character state changes inferred from comprehensive and democratic datasets of 19 pollen morphological and two ecological characters for lineages at or above family level in monocots analyzed with Fitch parsimony (FP), maximum likelihood (ML), and hierarchical Bayesian inference (HB). Pollen characters and their states (in brackets) correspond to Table 1. Superscripts refer to the number of the method used: ¹CFP, ²CHB, ³DFP, ⁴DML, and ⁵DHB.

Taxon	Characters and states	
	Pollen characters	Ecological characters
Acorales	7 (0 ¹²⁴), 14 (2 ¹³⁴⁵), 17 (1 ²³⁴⁵)	21 (3 ²)
Alismataceae	3 (2 ⁴), 4 (1 ²⁵), 5 (1 ²⁵), 6 (0 ²⁵), 7 (0 ⁵), 8 (4 ²⁴⁵), 11 (1 ²⁵), 14 (2 ¹³⁵), 15 (1 ¹²³⁴⁵), 17 (1 ²³⁴⁵)	
Alismatales	None	
Alismatids	2 (0 ²⁴⁵), 3 (1 ²), 4 (1 ³), 6 (0 ⁵ , 2 ²), 7 (4 ²⁵), 8 (0 ²⁴⁵)	20 (3 ²), 21 (3 ¹²)
Alstroemeriaceae	7 (2 ⁵), 17 (3 ⁵)	
Amaryllidaceae	6 (2 ²), 7 (2 ⁵)	
Araceae	14 (2 ¹³⁴⁵), 17 (1 ²³⁴⁵)	
Arecales	2 (2 ²⁴⁵), 4 (1 ⁴), 6 (2 ²), 9 (2 ²⁴), 11 (2 ²), 14 (2 ⁵), 15 (1 ²), 17 (1 ²⁵)	
Asparagaceae	None	
Asparagales	None	
Asparagales–commelinids	10 (0 ⁴)	
Asparagales with Orchidaceae excluded	None	
Astelioids	None	20 (5 ²)
Boryaceae	14 (1 ²)	
Bromeliaceae	6 (1 ²⁴), 7 (2 ⁵)	20 (5 ¹)
Colchicaceae	15 (1 ²⁵), 17 (1 ⁵)	
Commelinaceae	7 (2 ²⁵)	
Commelinaceae–Hanguanaceae	2 (0 ²), 3 (1 ²⁵), 7 (0 ⁵), 13 (0 ²⁵)	
Commelinales	6 (1 ⁵)	
Commelinales–Zingiberales	7 (2 ⁵ , 3 ²), 8 (0 ²), 13 (0 ²⁵)	21 (2 ¹)
Commelinales–Zingiberales–Poales	3 (1 ¹²⁵), 4 (1 ²⁴), 5 (0 ²⁵)	21 (2 ²)
Commelinids	4 (1 ²⁵), 10 (0 ¹³)	
Commelinids with Arecales excluded	6 (2 ²), 7 (2 ⁵), 9 (0 ⁵), 14 (2 ¹)	
Core asparagoid	None	
Cyclanthaceae	None	
Cyclanthaceae–Pandanaeae	3 (1 ¹⁴), 4 (1 ¹²³⁴), 5 (0 ⁵), 10 (0 ¹³⁴), 11 (1 ¹³⁴), 14 (2 ³⁴), 17 (1 ³⁴)	
Cyperaceae	3 (2 ²⁵)	21 (2 ²)
Cyperids	1 (1 ¹²³⁴⁵), 6 (0 ²), 7 (0 ²⁵), 11 (1 ¹³), 14 (2 ⁴), 15 (1 ⁴), 16 (0 ²⁵), 17 (0 ²⁵ , 1 ⁴)	21 (2 ²)
Dasypogonales	7 (2 ⁴), 14 (2 ⁴⁵), 17 (1 ²⁴⁵)	
Dioscoreaceae	9 (2 ²), 14 (2 ³⁴⁵), 17 (1 ⁵)	
Dioscoreales	5 (1 ⁵), 9 (2 ²⁵), 10 (1 ⁵ , 2 ²), 16 (1 ²)	
Dioscoreales–Pandanales	None	
Eriocaulaceae–Xyridaceae	2 (0 ²⁵), 6 (1 ⁵), 14 (1 ²)	21 (3 ²)
Graminids	None	
Haemodoraceae–Pontederiaceae	2 (2 ²⁵), 7 (2 ⁵ , 3 ²), 8 (2 ³⁴ , 3 ²), 14 (2 ⁵)	21 (0 ²)
Ixioliriaceae–Tecophilaeaceae	6 (1 ⁵), 10 (2 ⁴), 14 (2 ⁵), 17 (3 ²⁵)	
Juncaceae	None	
Liliaceae	6 (2 ⁴)	
Liliales	6 (2 ¹³)	
Lowiaceae–Strelitziaceae	7 (2 ² , 3 ⁴⁵)	
Melanthiaceae	2 (0 ²⁵), 13 (0 ⁵), 19 (0 ⁵)	
Monocots	6 (1 ³⁴⁵), 7 (0 ³⁵), 9 (0 ⁵), 10 (0 ²⁵), 14 (1 ²)	
Monocots–magnoliids	6 (2 ⁵)	
Musaceae–Heliconiaceae	None	
Nartheciaceae	7 (0 ⁵), 10 (2 ²⁵), 17 (1 ²)	
Orchidaceae	10 (2 ²⁵), 11 (1 ²)	
Pandanaeae	5 (1 ² , 2 ⁵), 6 (2 ²), 7 (0 ³⁴⁵), 12 (1 ²⁵), 13 (1 ⁵), 17 (0 ⁵)	20 (4 ²)
Pandanales	14 (2 ⁵)	

Table 2. Continued.

Taxon	Characters and states	
	Pollen characters	Ecological characters
Petermanniaceae–Alstroemeriaceae– Colchicaceae	17 (5 ²⁵)	
Petrosaviales	7 (0 ²⁴⁵), 14 (0 ³)	21 (2 ³)
Philesiaceae–Rhipogonaceae	2 (0 ²⁵), 3 (1 ²⁵), 4 (1 ³), 6 (1 ³), 8 (0 ²), 15 (1 ³), 17 (0 ²⁵)	
Philydraceae–Haemodoraceae– Pontederiaceae	8 (2 ²⁵), 13 (1 ³)	
Poaceae	10 (2 ⁴), 16 (0 ²⁵), 17 (0 ⁴)	
Poales	3 (1 ⁴), 5 (1 ²⁵), 6 (0 ³), 11 (1 ²⁵)	
Poales with Bromeliaceae and Typhaceae excluded	11 (1 ⁴), 14 (2 ³), 15 (1 ²⁵), 17 (1 ²⁵)	20(1 ³)
Restiids	10 (2 ³), 17 (1 ³)	
Restiids–graminids	6 (0 ²), 11 (1 ¹³), 12 (1 ¹²³⁴⁵), 15 (1 ⁴), 17 (1 ⁴)	20(1 ⁴)
Stemonaceae	14 (0 ³ , 1 ³)	
Thurniaceae	7 (0 ¹⁴), 16 (1 ³), 17 (0 ⁴)	20(1 ⁴), 21(2 ¹)
Tofieldiaceae	2 (2 ⁴), 8 (2 ⁴)	
Typhaceae	3 (1 ²⁵), 4 (1 ²⁵), 6 (0 ²⁵), 11 (1 ¹²³⁴⁵)	20(1 ³), 21(3 ¹²)
Velloziaceae	7 (0 ¹²³⁴⁵), 10 (2 ²⁵), 14 (1 ³), 17 (3 ³)	
Xanthorrhoeaceae	6 (1 ³)	
Xyridaceae	3 (1 ³), 5 (2 ³), 7 (2 ²⁵), 8 (0 ²⁵), 13 (0 ²⁵), 19 (1 ²⁵)	
Zingiberaceae–Costaceae	3 (2 ²⁵), 7 (3 ³), 8 (4 ³), 13 (1 ²⁵)	
Zingiberales	2 (0 ²⁴⁵), 3 (1 ⁴), 4 (1 ³ , 2 ³), 6 (0 ²⁵), 7 (2 ⁴), 8 (0 ¹³⁴⁵), 13 (0 ¹³⁴), 14 (2 ³), 19 (0 ¹²³⁴⁵)	

Topology G possesses the fewest steps for basic shape, shape class, and outline in polar view (amb), of the three topologies (G–I) that focus on the basalmost branching group of Poales.

To illustrate character state changes throughout the phylogeny of monocots, we mapped the unambiguous character state changes in the 19 pollen characters and two ecological characters (Table 1) at internal nodes based on CHB optimization (Fig. 7), the method that tends to produce the fewest equivocal states at internal nodes in our analysis (Fig. 7). Changes in pollen character states were not distributed regularly but were clustered in certain lineages. While most nodes were associated with five or fewer changes, 14 internal nodes displayed at least five inferred changes; 10 nodes were seen with five changes, one node with six changes, two nodes with seven changes, and one node with nine changes. The 10 nodes with five changes include the root nodes of alismatids, the Stemonaceae, Commelinales, Zingiberales, and Typhaceae. The one node with six changes was the root of Xyridaceae. The two nodes with seven changes were the clade comprising Eriocaulaceae and Xyridaceae, and the Arecales. The root node of Alismataceae displayed nine changes.

Five orders displayed more than 20 internal pollen character state changes: Alismatales (41 changes), Asparagales (24), Liliales (21), Pandanales (22), and

Poales (45). In contrast, the Dioscoreales, Arecales, and Dasypogonales possessed very few or no changes: four, three, and zero, respectively. Taking the relative sampling and taxonomic size of a lineage into account (pollen character state changes per internal node within a clade), the highest relative rate of pollen character state changes was found in Alismatales, Commelinales, and Arecales (3.73, 3.25, and 3, respectively), while Zingiberales, Asparagales, and Dasypogonales had the lowest relative rate of pollen character change (1.17, 0.83, and 0, respectively).

Thus, these 19 pollen characters (Table 1) showed variable frequencies of state change during the evolution of monocots. Changes of character state at internal nodes were found to be more frequent in pollen size (char. 7, with 29 changes), pollen outline in polar view (char. 6, 22 changes), and tectum sculpture (char. 17, 23 changes), whereas pollen dispersal unit (char. 1, one change), annulus (char. 12, two changes), infratectum structure (char. 18, one change), and pollen foot layer (char. 19, two changes) had far fewer (Fig. 7).

ANALYSES OF CORRELATED EVOLUTION

With the exception of exine presence (MCMC method, log Bayes factor value [log BF] = 3.19), we failed to find positive correlations between exine stratification states and hydrophytes using ML and

Table 3. Results of correlated evolution analyses using maximum likelihood (ML) and Markov chain Monte Carlo (MCMC) methods. Characters and character states are numbered, following Table 1.

Trait pair (pollen and ecological character)	ML			MCMC		
	Likelihood			Harmonic mean of log-likelihood		
	Independent model	Dependent model	Likelihood ratio (LR)	Independent model	Dependent model	Log Bayes factor (LBF)
Exine stratification and helo–hydrophytes						
Exine (character [char.] a1) and helo–hydrophytes (char. b1)	−94.01	−87.12	13.77†	−99.27	−92.71	13.12‡
Tectum (char. a2) and helo–hydrophytes (char. b1)	−102.50	−95.33	14.33†	−106.99	−102.53	8.93†
Eutectum (char. a3) and helo–hydrophytes (char. b1)	−146.43	−142.33	8.22	−150.63	−149.21	2.85*
Infractectum (char. a4) and helo–hydrophytes (char. b1)	−98.90	−92.20	13.40†	−104.04	−101.73	4.62*
Columellae (char. a5) and helo–hydrophytes (char. b1)	−109.91	−105.22	9.38	−113.62	−113.72	−0.20
Granules (char. a6) and helo–hydrophytes (char. b1)	−82.80	−82.33	0.93	−89.06	−88.87	0.39
Exine stratification and hydrophytes						
Exine (char. b1) and hydrophytes (char. b2)	−68.09	−63.61	8.96	−71.20	−69.60	3.19*
Tectum (char. a2) and hydrophytes (char. b2)	−76.58	−73.15	6.86	−78.49	−78.20	0.57
Eutectum (char. a3) and hydrophytes (char. b2)	−120.51	−118.61	3.82	−126.46	−125.69	1.54
Infractectum (char. a4) and hydrophytes (char. b2)	−72.97	−70.11	5.74	−75.75	−75.33	0.83
Columellae (char. a5) and hydrophytes (char. b2)	−83.99	−81.69	4.60	−87.19	−87.59	−0.81
Granules (char. a6) and hydrophytes (char. b2)	−56.88	−56.63	0.49	−61.87	−62.19	−0.65

* $P < 0.05$, LBF > 2 .
† $P < 0.01$, LBF > 5 .
‡ $P < 0.005$, LBF > 10 .

MCMC analysis methods (Table 3). ML and MCMC analyses of correlation for the eutectum and helo–hydrophily yielded inconsistent results ($P > 0.05$, log BF = 2.85, Table 3).

There was very strong or strong support for correlated evolution between exine presence and habitat for helo–hydrophytes (both with significance of $P < 0.01$ and log BF > 10), and strong or positive support for correlated evolution between three exine characters (presence of tectum, eutectum, and infractectum) and helo–hydrophily ($P < 0.01$, log BF = 5–10). The remaining two pollen traits tested (columellate infractectum and granular infractectum) were not significantly correlated with helo–hydrophily (a negative correlation with $P > 0.05$ and log BF < 2). Results of correlated evolution analyses for the seven pairs of traits are shown in Table 3.

In a test of specific hypotheses with regard to contingent evolution, significant support was found: the presence of pollen exine was not gained preferentially in helo–hydrophytes compared to those

that were not helo–hydrophytes (hypothesis q24 $<$ q13, probability values 0.02). Meanwhile, in a test of specific hypotheses of exclusiveness evolution, the loss of pollen exine was not significant in plants that were not helo–hydrophytes (hypothesis q31 = 0, probability values 0.1304) but was significant in helo–hydrophytes (hypothesis q42 = 0, probability values 0.0120). The losses of pollen tectum and infractectum were significant in both helo–hydrophytes and those that were not helo–hydrophytes (hypothesis q31 = 0 rejected, probability values 0.0347 and 0.0262 respectively, $P < 0.005$).

DISCUSSION

SYSTEMATIC SIGNIFICANCE OF POLLEN MORPHOLOGY IN MONOCOTS

Our optimizations using five methods (analysis of a comprehensive dataset with Fitch parsimony and hierarchical Bayesian inference [abbreviated as CFP

and CHB] and analysis of a democratic dataset with Fitch parsimony, maximum likelihood, and hierarchical Bayesian inference [abbreviated as DFP, DML, and DHB respectively]) allowed us to infer the pollen morphological state changes or synapomorphies for multiple branches within the monocot phylogenetic tree. We found that pollen characters may be of systematic value for delimiting lineages and may provide clues to controversial relationships within monocots (cf. Table 2). Each of the major lineages of monocots is discussed below.

Acorales. The order Acorales was recognized in both Angiosperm Phylogeny Group II (2003) and Angiosperm Phylogeny Group III (2009) classifications. *Acorus*, the single genus in the order, was previously placed in Araceae (reviewed in Grayum, 1987) but later found to be sister to the rest of the monocots based on molecular data (e.g., Chase et al., 1993; Duvall et al., 1993a, 1993b; Chase et al., 2006; Graham et al., 2006). Its isolated position is strongly congruent with several synapomorphies, including small size (char. 7, CFP, CHB, and DML), eutectate pollen (char. 14, CFP, DFP, DML, and DHB), and perforate tectum (char. 17, CHB, DFP, DML, and DHB) (Table 2).

Alismatales. The large order Alismatales comprises ca. 4560 herbaceous species of aquatic and moist habitats and is the second-diverging clade within the monocots (Angiosperm Phylogeny Group III, 2009). No unambiguous pollen synapomorphies were found for the Alismatales. Recent molecular phylogenetic estimates have identified three major clades within Alismatales: Araceae, Tofieldiaceae, and the alismatid aquatic families (Chen et al., 2004a, 2004b; Chase et al., 2006), all of which are characterized by character state changes. For Araceae, states include pollen eutectate (char. 14, CFP, DFP, DML, and DHB) with perforate tectum (char. 17, CHB, DFP, DML, and DHB); Tofieldiaceae are characterized by isopolar and diaperturate pollen (char. 2 and char. 8, DML). Character states identified for the aquatic alismatid families are pollen apolar (char. 2, CHB, DML, and DHB), radially symmetrical in polar view (char. 3, CHB), globose (char. 4, CHB and DHB), circular in polar view (char. 6, DHB), gigantic in size (char. 7, CHB and DHB), and lacking apertures (char. 8, CHB, DML, and DHB; Table 2).

Petrosaviales. The family Petrosaviaceae (Kubitzki, 1998a) was newly recognized as the order Petrosaviales in Angiosperm Phylogeny Group III (2009). Most members of the group were previously

treated as belonging to a diversity of families including Liliaceae (Ohba, 1984), Nartheciaceae, Tofieldiaceae, and Melianthaceae (Dahlgren et al., 1985). The isolated position of this order is characterized by two pollen character state changes, to small pollen size (char. 7, CHB, DML, and DHB) and intectate pollen (char. 14, DHB; Table 2).

Dioscoreales and Pandanales. Dioscoreales are moderately supported as sister to Pandanales based on molecular evidence (Chase et al., 2006; Graham et al., 2006; Petersen et al., 2006). We found no palynological characters to support this relationship. The Dioscoreales themselves were characterized by three pollen character state changes, to spheroidal pollen (char. 5, DHB), equatorial apertures (char. 9, CHB and DHB), and echinate suprategular elements (char. 16, CHB). The monophyly of the Dioscoreaceae s.l. (including the former Taccaceae and Trichopodaceae, as accepted by the Angiosperm Phylogeny Group II based on the combined molecular-morphological analyses of Caddick et al. [2000, 2002a, 2002b]) is congruent with state changes to equatorial apertures (char. 9, CHB), eutectate pollen (char. 14, DFP, DML, and DHB), and perforate tectum sculpture (char. 17, DHB). Pollen morphology is particularly congruent with known systematic relationships within Pandanales. The sister relationship between Cyclanthaceae and Pandanaceae is congruent with pollen character state transitions to radial symmetry (char. 3, CFP and DML), globose shape (char. 4, CFP, CHB, DFP, and DML), oblate pollen (char. 5, CHB), smooth aperture membrane (char. 10, CFP, DFP, and DML), porate apertures (char. 11, CFP, DFP, and DML), eutectate pollen (char. 14, DFP and DML), and a perforate tectum (char. 14, DFP and DML). Pandanaceae as a group are defined by oblong outline in polar view (char. 6, CHB), small size (char. 7, DFP, DML, and DHB), annulus present (char. 12, CHB and DHB), atectate pollen (char. 13, DHB), and imperforate tectum sculpture (char. 17, DHB). Stemonaceae received no defining pollen character states, while Velloziaceae are characterized by small pollen size (char. 7, all five methods) with an operculum (char. 10, CHB and DHB), semitectate (char. 14, CHB), and rugulate tectum (char. 17, CHB; Table 2).

Liliales. Only one pollen character state change, to oblong outline in polar view (char. 6, CFP and DFP), is found on the stem of Liliales. The recent merger of Luzuriagaceae into Alstroemeriaceae (Mabberley, 2008; Angiosperm Phylogeny Group III, 2009) is congruent with both large pollen size (char. 7, DHB) and rugulate tectum (char. 17, DHB).

The placement of Uvulariaceae within Colchicaceae (Fay et al., 2006) is congruent with suprategal elements present (char. 15, CHB and DHB) and perforate tectum sculpture (char. 17, DHB). The placement of the Petermanniaceae has been debated for some time (Angiosperm Phylogeny Group II, 2003; Janssen & Bremer, 2004; Fay et al., 2006). The topology we used in our study, in which it is sister to the clade comprising Alstroemeriaceae and Colchicaceae (Fay et al., 2006), is congruent with two pollen character state transitions, to large size (char. 7, DHB) and fossulate tectum (char. 17, CHB and DHB; Table 2).

Asparagales. The placement of Asparagales as sister to commelinids has been moderately supported by Chase et al. (2006) and strongly by Graham et al. (2006). In our study, this relationship is congruent with only one pollen state (char. 10, smooth aperture membrane, DHB). No state change was found to occur on the branch leading to Asparagales. The monophyly of the astelioid clade (including Asteliaceae, Blandfordiaceae, Boryaceae, Hypoxidaceae, and Lanariaceae) has been well supported in recent phylogenetic studies (Seberg et al., 2012; Chen et al., 2013); however, no pollen character state changes were found for this clade. The placement of Ixioliriaceae as sister to Tecophilaeaceae was strongly supported in the study of Chen et al. (2013) and is congruent with transitions to elliptic pollen outline in polar view (char. 6, DHB), operculate aperture (char. 10, DML), eutectate pollen (char. 14, DHB), and rugulate tectum (char. 17, CHB and DHB; Table 2).

Commelinids. The commelinid clade is strongly supported in molecular studies (reviewed in Chase et al., 2006), and the monophyly of each of the five commelinid orders is well established (e.g., Davis et al., 2004; Chase et al., 2006). However, internal relationships among its five major groups remain controversial, particularly the positions of Dasypogonales and Arecales (e.g., Chase et al., 2006; Graham et al., 2006; Givnish et al., 2006, 2010; Angiosperm Phylogeny Group III, 2009; Soltis et al., 2011; Barrett et al., 2012; Davis et al., 2012). Six main conflicting topologies within the commelinids are summarized in Figure 1.

Among the six alternative topologies tested (A–F), topologies A, D, and E produced the minimum number of pollen character state change steps in the CFP analysis, and, thus, they are inferred to be favored by pollen morphology based on the parsimony theory, i.e., ((Arecales (Dasypogonales (Commelinales–Zingiberales, Poales))), ((Arecales, Dasypogonales) (Commelinales–Zingiberales, Poales)), and

((Arecales, Poales) (Commelinales–Zingiberales, Dasypogonales))), respectively (Fig. 1). It is noteworthy that the latest phylogenetic studies using plastid genes and genomes (Givnish et al., 2010; Barrett et al., 2012; Davis et al., 2012) support Arecales plus Dasypogonales as sister to the rest of the commelinid monocots (topology D).

The sister relationship between Commelinales and Zingiberales has been well supported (Chase et al., 2006; Givnish et al., 2006, 2010; Graham et al., 2006; Soltis et al., 2007, 2011; Qiu et al., 2010) and is also congruent with transitions to very large or large size (char. 7, CHB and DHB, respectively), inaperturate (char. 8, CHB) and exineless pollen (char. 13, CHB and DHB; Table 2). Both topologies A and D contain a clade comprising Commelinales and Zingiberales as sister to Poales, which is characterized by radial symmetry (char. 3) in both.

The studies of both Givnish et al. (2006) and Chase et al. (2006) presented consistent sister relationships between Haemodoraceae and Pontederiaceae. The clade comprising Haemodoraceae and Pontederiaceae is congruent with multiple pollen character state changes, to isopolar pollen (char. 2, CHB and DHB), very large size or large size (char. 7, CHB and DHB, respectively), two apertures (char. 8, DFP and DML), and eutectate grains (char. 13, DHB; Tables 1, 2).

The Zingiberales are a well-characterized clade with nine inferred shared pollen character states: apolar (char. 2, CHB, DML, and DHB), radially symmetrical (char. 3, DML), globose pollen (char. 4, CHB), circular outline in polar view (char. 6, CHB and DHB), large size (char. 7, DML), no apertures (char. 8, CFP, DFP, DML, and DHB), no exine (char. 13, CFP, DFP, and DML), eutectate pollen (char. 14, DHB), and no foot layer (char. 19, all five methods). Two pairs of sister families are found within the order: Costaceae and Zingiberaceae, and Lowiaceae and Strelitziaceae (Kress et al., 2001; Chase et al., 2006; Givnish et al., 2006). The former pairing is congruent with transitions to asymmetrical pollen (char. 3, CHB and DHB), very large size (char. 7, DHB), more than three apertures (char. 8, CFP, DFP, DML, and DHB), exineless (char. 13, CFP, DFP, and DML) and eutectate pollen (char. 14, DHB), and absence of the foot layer (char. 19, all five methods); the latter pairing is congruent only with very large pollen size (char. 7, DML and DHB). The monophyletic group including Cannaceae, Marantaceae, Costaceae, and Zingiberaceae among other Zingiberales is congruent with one pollen character state change, to large pollen size (char. 7, CHB; cf. Fig. 1, Tables 1, 2).

Within Poales, the basalmost branching group has variously been recovered as Bromeliaceae, Typhaceae, or Bromeliaceae–Typhaceae (Davis et al., 2004; Chase et al., 2006; Givnish et al., 2006, 2010; Graham et al., 2006). These three conflicting basal topologies within Poales are shown in Figure 1G–I. Of these, topology G, with Bromeliaceae as the first lineage to diverge, and Typhaceae sister to the remaining Poales (including Rapateaceae and the graminid, restiid, cyperid, and xyrid clades) requires the fewest pollen character state changes (cf. Fig. 1G–I, Table 1). This topology, which is consistent with the phylogenetic work of Givnish et al. (2010), is inferred to be favored by pollen morphology.

The cyperid clade (including Cyperaceae, Juncaceae, and Thurniaceae) has been well supported by molecular data (Chase et al., 2006; Givnish et al., 2010) and can be characterized by pollen states including grains borne in tetrads (char. 1, all five methods), pollen circular outline in polar view (char. 6, CHB), small grain size (char. 7, CHB and DHB), porate aperture (char. 11, CFP and DFP), supratectal elements present (char. 15, DML), gemmate supratectal element shape (char. 16, CHB and DHB), and imperforate tectum (char. 17, CHB and DHB). Herein, the pseudomonads of Cyperaceae are treated as hidden tetrads. The xyrids (including Eriocaulaceae, Mayacaceae, and Xyridaceae) did not form a monophyletic group in Chase et al. (2006) and our study (Fig. 7). We found that a sister relationship between Eriocaulaceae and Xyridaceae would be characterized by apolar pollen (char. 2, CHB and DHB), elliptic outline in polar view (char. 6, DHB), and semitectate pollen (char. 14, CHB). Mayacaceae can be distinguished from the other two families by its monosulcate and tectate to intectate pollen (Zavada, 1983), while there is no pollen character linking it with Eriocaulaceae and Xyridaceae. A sister relationship between the restiid and graminid clades is found to be congruent with pollen character state changes to circular outline in polar view (char. 6, CHB), porate aperture (char. 11, CFP and DFP) with an annulus (char. 12, all five methods), supratectal elements present (char. 15, DML), and perforate tectum sculpture (char. 17, DML; cf. Fig. 7, Tables 1, 2).

THE RELATIONSHIP BETWEEN MONOCOTS AND BASALLY BRANCHING ANGIOSPERMS

The Chloranthaceae, magnoliids, monocots, Ceratophyllaceae, and eudicots are all well supported as major lineages within angiosperms, but the relationships among them remain unclear (e.g., Qiu et al., 2005, 2006, 2010; Soltis et al., 2005, 2008, 2011;

Moore et al., 2007). Studies have suggested several alternatives for the closest relatives of monocots, ranging from magnoliids (Hilu et al., 2003; Duvall et al., 2006) to the aquatic Ceratophyllaceae (Qiu et al., 1999, 2005; Zanis et al., 2002), Ceratophyllaceae–eudicots (Moore et al., 2007; Soltis et al., 2011), Piperales (Duvall, 2000), or Laurales (Parkinson et al., 1999). In our study, although a sister relationship between monocots and magnoliids is congruent with shared pollen character states including oblong outline in polar view (char. 6, DHB; cf. Fig. 7, Table 1), an affinity of monocots to basal eudicots or Ceratophyllaceae has also been supported by pollen characters (Lu et al., 2015).

Our studies suggest that convergent evolution in pollen character states occurs commonly between some monocots and basally branching angiosperms. Both Lu et al. (2015) and the present study suggest that both groups contain taxa with inaperturate pollen grains with a highly reduced exine and thick channeled intine (Zingiberales and Lauraceae; Stone, 1987), trichotomosulcate pollen (Iridaceae, Arecaceae, and Chloranthaceae; Chapman, 1987; Goldblatt & Le Thomas, 1992, 1997; Harley, 1999) or pollen with zonate apertures (Araceae, Arecaceae, Nymphaeaceae, and Eupomatiaceae; Woodland & Garlick, 1982; Grayum, 1992; Gabarayeva & Rowley, 1994; Hesse et al., 2001; Harley & Dransfield, 2003). Polyplacate striae are found in Araceae, Zingiberaceae, and Lauraceae (Hesse et al., 2000), and loss or reduction of exine is also common in both monocots and basal angiosperms.

EVOLUTION OF POLLEN IN MONOCOTS

In this study, plesiomorphic pollen morphological states for monocots were unambiguously inferred under all five optimization methods to include pollen dispersal as monads (char. 1, Table 1, Fig. 7), pollen heteropolarity (char. 2), medium size (char. 7), monosulcate apertures (characters 8 and 11) with a sculptured aperture membrane (char. 10) and lacking an annulus (char. 12), exine fully present (char. 13), supratectal elements absent (char. 15), infratectum structure columellate (char. 18), and foot layer present (char. 19). The earliest monocot pollen is therefore likely to have been characterized by most of these pollen features.

Distal monosulcate pollen has long been considered an ancestral state for both basal angiosperms and monocots (Wodehouse, 1936; Takhtajan, 1969; Zavada, 1983; Sampson, 2000; Doyle, 2005; Lu et al., 2015). This character is also shown unambiguously to be plesiomorphic in monocots under four of our five methods (the exception being DHB, which

inferred an equatorial aperture position to be plesiomorphic), and this is in agreement with previous studies (Penet et al., 2005; Ressayre et al., 2005).

Evolution of the pollen dispersal unit (char. 1, Table 1, Fig. 7), infratectum structure (char. 18), and foot layer presence (char. 19) has been relatively conservative throughout the angiosperms (Wortley et al., 2015). These three pollen characters were found to be similarly stable in the evolution of monocots, having the lowest frequency of character state changes, despite the Orchidaceae (although here with only three taxa sampled) being noted as most diverse for pollen dispersal unit among angiosperms (Pacini & Hesse, 2002). Thus, the states dispersal as monads, columellate infratectum structure, and presence of a foot layer are found in the overwhelming majority of monocots. Other character states are less commonly reported (e.g., granulate infratectum) or are restricted to certain derived, monophyletic groups (e.g., absence of the foot layer in Haemodoraceae; Simpson, 1983). In contrast, pollen size (char. 7) and tectum sculpture (char. 17) displayed greater frequency of change among monocots, as has also been the case throughout angiosperms (Wortley et al., 2015).

Pollen aperture characters have displayed frequent state changes throughout the phylogeny of monocots. Although the range of aperture types in monocots is fewer than that observed for other angiosperms (Harley & Zavada, 2000), apertures are key to the evolution of monocot pollen morphology. Two aperture character state shifts, from a proximal to a distal position in early seed plant evolution and to an equatorial position seen at the base of the eudicot clade, have been regarded as some of the most striking innovations in the evolutionary history of seed plants (Muller, 1970; Walker & Doyle, 1975; Chanda & Ghosh, 1979; Zavada, 1983, 1984a; Rudall & Bateman, 2007). There is no intermediate position of apertures between distal and equatorial, and the switch in position reflects developmental changes expressed during meiosis (Blackmore & Crane, 1998). In our analyses for monocots, under CHB, a further transition from distal to equatorial apertures is inferred at the root of the Arecaceae. Pollen grains ascribed to Arecaceae are abundant and widely distributed from the Late Cretaceous (Burnham & Johnson, 2004; Nichols & Johnson, 2008) and include all four types of equatorial aperture found among monocots, from disulcate, found, for example, in Tofieldiaceae, Dioscoreaceae, and Liliaceae; to diporate, as seen in Bromeliaceae and Haemodoraceae; zonate, observed in Araceae,

Iridaceae, and Rapateaceae (Hesse & Zetter, 2005); and triaperturate, observed in Iridaceae, Commelinaceae, and Orchidaceae (Harley, 2004). Further extensive sampling and analysis of pollen morphology of the Arecaceae and related taxa will provide valuable clues to our understanding of distal/equatorial aperture transitions within angiosperms.

Zavada (1983) identified a number of evolutionary trends in aperture type in the monocots, such as the loss of a sulcus and an increase in the number and types of apertures. The trend of loss of sulcus was further exemplified by both Furness and Rudall (2006) and our CHB analysis. Furness and Rudall (2006) revealed that there are apparently homoplastic trends in each family toward either reduction in aperture size (e.g., from sulci to pores) or to coverage of the aperture with exine (e.g., from monosulcate to monosulcate-operculate) within Pandanales. In our analysis, monosulcate apertures were inferred unambiguously as plesiomorphic for monocots, whereas monoporate and inaperturate types were derived within the group. Monoporate pollen (char. 8 and char. 11) is inferred to have evolved on the branches leading to Cyclanthaceae–Pandanales (CFP, DFP, and DML), Typhaceae (all five methods), cyperids (CFP and DFP), and the graminid–restiid clade (CFP and DFP; Table 2). Within the clade comprising Philydraceae, Haemodoraceae, and Pontederiaceae, monosulcate pollen reoccurs in all taxa of the basally placed family Philydraceae (Simpson, 1985a), with diaperturate (char. 8, DFP and DML) or triaperturate pollen (char. 8, CHB) evolving in the more derived Haemodoraceae–Pontederiaceae (Table 2). Alismatales, among the later-diverging lineages of Alismatales, are characterized by pantoporate pollen (char. 8, CFP, CHB, DFP, and DML). Inaperturate pollen (char. 8, Fig. 7, Table 1) evolved more frequently on lineages with helo–hydrophytic plants, such as alismatids (CHB, DML, and DHB) and within Zingiberales (CFP, DFP, DML, and DHB).

ECOLOGICAL ADAPTATIONS IN POLLEN MORPHOLOGY

Monocots display a high diversity of pollination types, including wind pollination (Poaceae and Cyperaceae, exceptionally insect pollination in bamboo grasses; Soderstrom & Calderon, 1971), water pollination (diverse seagrass lineages in Alismatales), and bird pollination (widespread across the eight families of the Zingiberales; Nur, 1976), as well as dispersal of aggregated pollen, usually by animal vectors (Orchidaceae; Harder, 2000). Each of these pollination types corresponds to a series of distinct pollen features. For example, bird-pollinated Zingiberales possess exineless pollen with a thick-

ened, elaborated intine to preserve water (Kress & Stone, 1982; Theilade & Theilade, 1996); the water-pollinated seagrasses in Alismatales have filiform and exineless pollen (Ackerman, 1995, 2000); and the wind-pollinated graminid clade of Poales have typically distally monoporate pollen with an operculum and annulus (Linder & Rudall, 2005). It is interesting to note that the entomophilous bamboo genus, *Pariana* Aubl., has a unique pollen type without an annulus, which may imply a further possible association between pollen morphology and pollination type (Skvarla et al., 2003). In our CHB analysis, four internal nodes having not less than five changes in pollen character state were found to be closely associated with pollinator shifts: the root of the alismatids (from entomophily to hydrophily), the root of the Arecales (a reversal from ornithophily to entomophily), the root of Typhaceae (from ornithophily to anemophily), and the root of the clade comprising Eriocaulaceae and Xyridaceae (a reversal from anemophily to entomophily; see Fig. 7). The interesting results here indicate that the transitions in pollen morphological states may be potentially correlated with the shifts in pollination type.

Asparagales have the second highest diversification rate in monocots (Magallón & Castillo, 2009) yet the lowest average frequency of pollen character state changes at internal nodes among all orders except Dasypogonales (0.76). We found only 22 state changes across all 19 pollen characters studied in this clade: seven in pollen size (char. 7), four in outline in polar view (char. 6), three in aperture membrane (char. 6), four in tectum (char. 14), three in tectum sculpture (char. 17), and one in symmetry (char. 3), indicating that Asparagales pollen morphology has been consistent and comparatively stable during evolution (Fig. 7). In terms of ecological characters, habitat moisture (char. 21) was found to change frequently (seven times) within the core asparagoids, whereas pollination type (char. 20) did not change (Fig. 7): entomophily is consistently the most probable state under CHB at all internal nodes within Asparagales excluding the astelioids and Orchidaceae (Fig. 7). These observations suggest that changes in ecological interactions, particularly pollination type, may have remarkable impact as drivers of pollen morphological change within monocots, while pollen characters can remain remarkably stable under changing habitat moisture.

Fourteen internal nodes in the phylogeny of monocots were found to be characterized by a high number of pollen morphological state changes under CHB (Fig. 7, Table 1), including the root node of Alismataceae (nine changes); the root nodes of

Arecales (seven changes); the clade comprising Eriocaulaceae and Xyridaceae (seven changes); Xyridaceae (six changes); 10 further nodes have five changes, including the roots of alismatids, Stemonaceae, Commelinales, Zingiberales, and Typhaceae. Based on divergence time data for monocots provided by recent studies (Janssen & Bremer, 2004; Merckx et al., 2008; Bell et al., 2010; Smith et al., 2010; Bouchenak-Khelladi et al., 2014; Magallón et al., 2015), the crown or stem node ages of 10 of these 14 major clades are all dated to between 90 and 114 million years ago, approximately corresponding to the Albian-Turonian stage of the Middle Cretaceous. Although many monocot orders are unrepresented by fossil records during the Late Cretaceous, there is clear evidence that monocots were both diverse and widespread in the middle of the Late Cretaceous (Herendeen & Crane, 1995). The dramatic pollen character transformations in the Albian-Turonian seen in our analysis occurred contemporaneously with the rise of angiosperm-dominated ecosystems (Lidgard & Crane, 1990; Coiffard et al., 2006).

The functions of exine architecture in angiosperms are considered to be mainly protection (against adverse atmospheric conditions such as desiccation and UV radiation), storage of physiologically active substances, pollen grain clustering, and harmomegathy (Muller, 1979). It is likely in the near future that we will gain a fuller understanding of Heslop-Harrison's (1969, 1972) insights that pollen wall patterning is not directly coded by genes but involves an interplay between the products of gene expression and the influence of physical forces (Blackmore et al., 2007). Water content status influences not only the survival, longevity, and germination ability of angiosperm pollen (Franchi et al., 2002; Aylor, 2003), but also their exine stratification: exine reduction or loss in monocots has been associated with moist or aquatic environments (Heslop-Harrison, 1976; Philbrick, 1991; Furness & Rudall, 1999; Tanaka et al., 2004), such as those frequented by many alismatids (Thanikaimoni, 1978). However, the complexity of the exine and the development of its stratification under physical stress may limit our understanding of the associations between exine architecture and habitat moisture. We confirmed that three exine stratification traits (exine, tectum, and infratectum) are correlated with the evolution of helo-hydrophytic habitat (Table 3, Fig. 2). The presence or absence of exine is most strongly correlated with helo-hydrophytic habitat rather than hydrophytic habitat among six exine structures (Table 3, Fig. 2). Furthermore, tests of contingent evolution indicated that exine absence was not preferentially lost in helo-

hydrophytes of moist to wet habitats. All of these results indicate that habitat moisture may provide a selective pressure that crucially affects the evolution of pollen morphology in monocots.

Granular infratectum structure appears to be derived within monocots, as the more basally branching lines have a columellate infratectum (Doyle, 2009).

We confirmed that a columellate infratectum is unambiguously plesiomorphic under all five optimization methods. However, neither the ancestral columellate infratectum nor the derived granulate version is found to be significantly correlated with preference for a helo–hydrophytic habitat (Table 3, Fig. 2). Zavada (1983) proposed that a primitive tectate-columellate (perforate or imperforate) wall structure type gave rise to monocotyledonous atectate walls or granular infratectum and finally extreme reduction of the exine, in which it may be completely absent. Our results indicate that the loss of infratectum structure may play a part in the *process* of exine reduction, which leads to subsequent morphological adaptations to helo–hydrophytic habitat.

FUTURE PROSPECTS

Although more extant and fossil pollen morphological data may facilitate a better understanding of pollen evolution and diversification, a more robust phylogenetic framework for monocots based on increased genetic data and denser taxon sampling may also be required for future reconstruction of pollen characters. In particular, there is a need for a better resolution of the positions of Dasypogonales and Arecales, as well as for internal relationships within Commelinales and Zingiberales, and the basalmost-branching group of Poales. In this paper, evolutionary patterns have emerged with respect to pollen characters of monocots, identifying a number of unambiguous pollen plesiomorphies and character state changes, revealing correlations with pollination type and habitat moisture using FP, ML, and HB methods. Substantial clues to the understanding of pollen morphological transformations during the evolution of monocots (e.g., pollen polarity transitions within Arecaceae) may help in elucidating correlations between exine reduction or loss and helo–hydrophytes in moist to wet habitats in the evolution of monocots (as well as in other angiosperms). Past interpretations of the evolutionary significance of fossil pollen have relied heavily on comparative morphological studies of extant pollen (Zavada, 1983). Our optimization techniques demonstrate that dramatic state changes in pollen morphology oc-

curred across the monocot phylogeny in the Albian-Turonian stage, which may provide insights for interpreting enigmatic early monocot pollen evolution.

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Appendix 1. Phylogenetic position and terminal taxa used in the phylogenetic analyses (in order to be consistent with the taxa used in Chase et al. [2006], both *Acorus calamus* L. and *A. gramineus* Sol. ex Aiton are listed). Generic totals for families are sensu the Angiosperm Phylogeny Group III (2009) and Chase et al. (2006). One hundred twenty taxa represent the 12 orders and 71 families of monocots, and 16 outgroup taxa represent the nine orders and 13 families of basal angiosperms considered in analysis. Twenty species are vouchers for pollen exemplars seen in Figures 3–6.

Taxonomic classification	Total # of genera per family (total # of genera sampled)	Taxon name, with species voucher	References and voucher information	
			References used for palynological data	References used for ecological data
Monocots				
ACORALES				
Acoraceae	1 (1)	<i>Acorus calamus</i> L.	Grayum, 1992; Rudall & Furness, 1997	Cook, 1990; Kubitzki, 1998b; Buzgo & Endress, 2000
		<i>A. gramineus</i> Sol. ex Aiton	Grayum, 1992; Rudall & Furness, 1997	Cook, 1990; Kubitzki, 1998b; Buzgo & Endress, 2000
		<i>A. gramineus</i> Sol. ex Aiton (Fig. 3A–C)	China, Yunnan, <i>S. D. Zhang et al. APE-LY-001</i> (KUN, living collection from KBG)	
ALISMATALES				
Alismataceae	15 (2)	<i>Alisma</i> L.	Argue, 1971, 1974, 1976; Punt & Reumer, 1981; Zavada, 1983; Chanda et al., 1988	Daumann, 1965; Björqvist, 1967; Cook, 1990; Kubitzki, 1998b
		<i>A. orientale</i> (Sam.) Juz. (Fig. 3G, H)	China, Shanxi, <i>L. Zhang & K. M. Lian Zhang f0031</i> (KUN)	
		<i>Sagittaria</i> L.	Argue, 1971, 1974, 1976; Punt & Reumer, 1981; Zavada, 1983; Chanda et al., 1988	Cook, 1990; Kubitzki, 1998b
Araceae	117 (3)	<i>Gymnostachys</i> R. Br.	Grayum, 1992; Hesse, 2006	Kubitzki, 1998b
		<i>Arisaema</i> Mart.	Wang & Zhao, 2002; Wang et al., 2002	Kubitzki, 1998b
		<i>Orontium</i> L.	Grayum, 1992; Weber et al., 1999; Hesse, 2006	Cook, 1990; Kubitzki, 1998b
		<i>Epipremnum pinnatum</i> (L.) Engl. (Fig. 1D–F)	Australia, Queensland, <i>L. J. Brass 19829</i> (CANB)	
Butomaceae	1 (1)	<i>Butomus</i> L.	Argue, 1971; Zavada, 1983; Chanda et al., 1988; Grayum, 1992; Perveen & Qaiser, 2003; Furness & Banks, 2010	Cook, 1990; Kubitzki, 1998b
Cymodoceaceae	5 (1)	<i>Cymodocea</i> K. D. Koenig	Li & Zhou, 2009	Cook, 1990; Kubitzki, 1998b
Hydrocharitaceae	18 (1)	<i>Vallisneria</i> L.	Sharma, 1968; Sun et al., 2002; Tanaka et al., 2004	Cook, 1990; Kubitzki, 1998b; Tanaka et al., 2004
Juncaginaceae	3 (1)	<i>Triglochin</i> L.	Cranwell, 1953; Wang, 1990; Grayum, 1992	Charlton, 1981; Cook, 1990; Kubitzki, 1998b
Potamogetonaceae	4 (1)	<i>Potamogeton</i> L.	Cranwell, 1953; Wang, 1990; Grayum, 1992; Perveen, 1999	Posluszny & Sattler, 1974; Cook, 1990; Kubitzki, 1998b
Tofieldiaceae	3 (2)	<i>Pilea</i> Michx.	Kosenko, 1987; Takahashi & Kawano, 1989	Kubitzki, 1998a; Li & Zhou, 2006

Appendix 1. Continued.

Taxonomic classification	Total # of genera per family (total # of genera sampled)	Taxon name, with species voucher	References and voucher information	
			References used for palynological data	References used for ecological data
Zosteraceae		<i>Tofieldia</i> Huds.	Huynh, 1976; Schulze, 1978; Kosenko, 1987; Takahashi & Kawano, 1989; Díaz et al., 1990; Furness & Banks, 2010	Kubitzki, 1998a; Li & Zhou, 2006
	1 (1)	<i>Zostera</i> L.	Pettitt et al., 1984; Díez et al., 1988; Furness & Banks, 2010	Cook, 1990; Kubitzki, 1998b
PETROSAVIALES		<i>Z. marina</i> L. (Fig. 3I, J)	Denmark, Zealand Island, <i>N. Jacobse & J. Svendsen</i> 484 (E)	
Petrosaviaceae	2 (2)	<i>Japonolirion</i> Nakai	Kosenko, 1987; Takahashi & Kawano, 1989; Caddick et al., 1998; Furness & Banks, 2010	Kubitzki, 1998a
		<i>Petrosavia</i> Becc.	Caddick et al., 1998; Handa et al., 2001; Furness & Banks, 2010	Kubitzki, 1998a
		<i>P. stellaris</i> Becc. (Fig. 3K, L)	Malaysia, Sarawak, <i>B. L. Burt & A. M. Martin</i> B5277 (E)	
DIOSCOREALES		<i>Dioscorea</i> L.	Radulescu, 1973; Zavada, 1983; Caddick et al., 1998; Schols et al., 2001, 2003, 2005	Fatokun et al., 1992; Kubitzki, 1998b
	4 (3)	<i>D. melanophyllum</i> Prain & Burkill (Fig. 4A, B)	China, Yunnan, <i>the Ailaoshan expedition team XPALSC550</i> (KUN)	
		<i>Tacca</i> J. R. Forst. & G. Forst.	Zavada, 1983; Caddick et al., 1998; Schols et al., 2005	Zhang et al., 2005
		<i>Trichopus</i> Gaertn.	Caddick et al., 1998	Kubitzki, 1998b
Nartheciaceae	4 or 5 (2)	<i>Alettris</i> L.	Kosenko, 1987; Takahashi & Kawano, 1989	Sullivan, 1973; Kubitzki, 1998a
		<i>Narthecium</i> Huds.	Takahashi & Kawano, 1989; Caddick et al., 1998; Handa et al., 2001; Schols et al., 2005	Jacquemart, 1996; Kubitzki, 1998a
PANDANALES		<i>Cyclanthus</i> Poit. ex A. Rich.	Harling, 1958; Eriksson, 1994a; Kubitzki, 1998a; Furness & Rudall, 2006	Beach, 1982; Kubitzki, 1998a
Cyclanthaceae	12 (4)	<i>Carludovica</i> Ruiz & Pav.	Harling, 1958; Eriksson, 1994a; Kubitzki, 1998a; Furness & Rudall, 2006	Eriksson, 1994b; Kubitzki, 1998a
		<i>Chorigyne</i> R. Erikss.	Eriksson, 1989, 1994a; Kubitzki, 1998a	Kubitzki, 1998a
		<i>Sphaeradenia</i> Harling	Harling, 1958; Zavada, 1983; Eriksson, 1994a; Furness & Rudall, 2006	Kubitzki, 1998a
	4 (2)	<i>Freycinetia</i> Gaudich.	Hotton et al., 1994; Furness & Rudall, 2006	Cox, 1990; Kubitzki, 1998a
Pandanaceae		<i>Pandanus</i> Parkinson	Huynh, 1980; Hotton et al., 1994	Cox, 1990; Kubitzki, 1998a

Appendix 1. Continued.

Taxonomic classification	Total # of genera per family (total # of genera sampled)	Taxon name, with species voucher	References and voucher information	
			References used for palynological data	References used for ecological data
Stemonaceae	4 (2)	<i>Groomia</i> Torr. <i>Stemona</i> Lour. <i>S. tuberosa</i> Lour. (Fig. 4C, D) <i>Acanthochlamys</i> P. C. Kao <i>Talbotia</i> Balf.	Van der Ham, 1991 Van der Ham, 1991; Furness & Rudall, 2006 China, Yunnan, <i>S. D. Zhang et al. APE-LY-017</i> (KUN, living collection from KBC) Gao, 1987 Furness & Rudall, 2006	Rogers, 1982; Kubitzki, 1998a Rogers, 1982; Kubitzki, 1998a Kubitzki, 1998a Kubitzki, 1998a
LILIALES				
Alstroemeriaceae	5 (2)	<i>Alstroemeria</i> L. <i>Luzuriaga</i> Ruiz & Pav. <i>Campynema</i> Labill.	Sarwar et al., 2010 Schulze, 1982a; Kosenko, 1994a Erdtman, 1952; Dutt, 1970; Goldblatt, 1986; Kosenko, 1987	Kubitzki, 1998a Kubitzki, 1998a Kubitzki, 1998a
Campynemataceae	2 (1)			
Colchicaceae	15 (2)	<i>Schelhammera</i> R. Br. <i>Uvularia</i> L.	Kosenko, 1988 Radulescu, 1973; Buchner & Weber, 2000 onwards	Kubitzki, 1998a Kubitzki, 1998a
Liliaceae	19 (2)	<i>Calochortus</i> Pursh <i>Lilium</i> L. <i>Tulipa iliensis</i> Regel (Fig. 4G–I) <i>Trillium</i> L. <i>T. maculatum</i> Raf. (Fig. 4E, F) <i>Veratrum</i> L. <i>Petermannia</i> F. Muell. <i>Philesia</i> Comm. ex Juss.	Heusser, 1971; Radulescu, 1973; Schulze, 1980b; Halbritter & Hesse, 1993; Kosenko, 1999 Radulescu, 1973; Schulze, 1980b; Halbritter & Hesse, 1993; Kosenko, 1999 China, Xinjiang, <i>D. Y. Tan DY0180</i> (KUN) Takahashi, 1982, 1983; Buchner & Weber, 2000 onwards U.S.A., Oklahoma, <i>R. K. Godfrey 84058</i> (IBSC) Buchner & Weber, 2000 onwards Erdtman, 1952; Schulze, 1982a Erdtman, 1952; Cranwell, 1953; Heusser, 1971; Schulze, 1982a; Cauneau-Pigot, 1988 Schulze, 1982b; Furness & Rudall, 1999; Chen et al., 2006 Chen et al., 2006; Kodela, 2006	Kubitzki, 1998a; Dilley, 1999 Kubitzki, 1998a Kubitzki, 1998a Mulligan & Munro, 1987; Kubitzki, 1998a Kubitzki, 1998a Kubitzki, 1998a Macmillan, 1972; Kubitzki, 1998a Kevan et al., 1991; Kubitzki, 1998a
Melanthiaceae	16 (2)			
Petermanniaceae	1 (1)			
Philesiaceae	2 (1)			
Rhipogonaceae	1 (1)	<i>Rhipogonum</i> J. R. Forst. & G. Forst. <i>Smilax</i> L.		
Smilacaceae	1 (1)			
ASPARAGALES				
Amaryllidaceae	73 (3)	<i>Allium</i> L. <i>A. cyaneum</i> Regel (Fig. 4J–L)	Nair & Sharma, 1965; Radulescu, 1973; Schulze, 1980a; Buchner & Weber, 2000 onwards; Guler & Pehlivan, 2006 China, Qinghai, <i>Y. H. Wu LJQ-QLS-2008-0158</i> (KUN)	Kubitzki, 1998a

Appendix 1. Continued.

Taxonomic classification	Total # of genera per family (total # of genera sampled)	Taxon name, with species voucher	References and voucher information	
			References used for palynological data	References used for ecological data
Asparagaceae	153 (11)	<i>Agapanthus</i> L'Her.	Nair & Sharma, 1965; Radulescu, 1973; Buchner & Weber, 2000 onwards	Leighton, 1965; Kubitzki, 1998a
		<i>Clivia</i> Lindl.	Afzelius, 1955; Gullvåg, 1964	Kubitzki, 1998a; Meerow & Clayton, 2004
		<i>Asparagus</i> L.	Nair & Sharma, 1965; Buchner & Weber, 2000 onwards; Özler & Pehlivan, 2008	Kubitzki, 1998a
		<i>Arthropodium</i> R. Br.	Radulescu, 1973	Kubitzki, 1998a
		<i>Convallaria</i> L.	Ma & Hong, 1990	Kubitzki, 1998a; Araki et al., 2005
		<i>Aphyllanthes</i> L.	Radulescu, 1973; Furness, 1985; Lifante et al., 1990	Kubitzki, 1998
		<i>Brodiaea</i> Sm.	Schulze, 1980a	Han et al., 1991
		<i>Scilla</i> L.	Radulescu, 1973; Schulze, 1980b; Chavami et al., 2009	Kubitzki, 1998a
		<i>Anemarrhena</i> Bunge	Chen & Qiao, 2000	Kubitzki, 1998a
		<i>Agave</i> L.	Alvarez & Köhler, 1987; Stroo, 2000	Gentry, 1982; Kubitzki, 1998a
Asteliaceae	1 (1)	<i>Chlorophytum</i> Ker Gawl.	Nair & Sharma, 1965; Buchner & Weber, 2000 onwards	Kubitzki, 1998a; Poulsen & Nordal, 2005
		<i>Behnia</i> Didr.	Schulze, 1982a; Conran, 1999	Kubitzki, 1998a
		<i>Herreria</i> Ruiz & Pav.	Kosenko, 2001	Kubitzki, 1998a
		<i>Astelia</i> Banks & Sol. ex R. Br.	Cranwell, 1953; Radulescu, 1973; Kosenko, 2001; APSA, 2007	Moore, 1966; Kubitzki, 1998a
		<i>Blandfordia</i> Sm.	Schulze, 1982b; Kosenko, 1994b	Zimmerman & Pyke, 1988; Kubitzki, 1998a
		<i>Alania</i> Endl.	Erdtman, 1952; Schulze, 1982b; APSA, 2007	Kubitzki, 1998a; Western Australian Herbarium, 1998 onwards
Blandfordiaceae	1 (1)			
Boryaceae	2 (2)			
Doryanthaceae	1 (1)	<i>Borya</i> Labill.	Erdtman, 1952; APSA, 2007	Keighery, 1984; Kubitzki, 1998a
		<i>Doryanthes</i> Corrêa	Schulze, 1982b; Buchner & Weber, 2000 onwards	Newman, 1929; Kubitzki, 1998a
		<i>Hypoxis</i> L.	Cranwell, 1953	Cook, 1990; Kubitzki, 1998a
		<i>Sisyrinchium</i> L.	Schulze, 1971; Nadot et al., 2006	Kubitzki, 1998a; Freitas & Sazima, 2003
		<i>Ixiolirion</i> Fisch. ex Herb.	Schulze, 1983; Donmez & Isik, 2008	Kubitzki, 1998a; Li & Zhou, 2006
		<i>Lanaria</i> Aiton	Erdtman, 1952	Kubitzki, 1998a
Lanariaceae	1 (1)	<i>Newwiedia</i> Blume	Schill, 1978	Benzing & Atwood, 1984; Okada et al., 1996
		<i>Cypripedium</i> L.	Burns-Balogh & Hesse, 1988	Benzing & Atwood, 1984; Davis, 1986
		<i>Epipactis</i> Zinn	Ackerman & Williams, 1980	Brantjes, 1981; Benzing & Atwood, 1984
		<i>Tecophilaea</i> Bertero ex Colla	Erdtman, 1952; Simpson, 1985b	Kubitzki, 1998a
Tecophilaeaceae	7 (1)			
Xanthorrhoeaceae	35 (3)	<i>Xanthorrhoea</i> Sm.	Chanda & Ghosh, 1976	Keighery, 1980; Kubitzki, 1998a

Appendix 1. Continued.

Taxonomic classification	Total # of genera per family (total # of genera sampled)	Taxon name, with species voucher	References and voucher information	
			References used for palynological data	References used for ecological data
Xeronemataceae ARECALES	1 (1)	<i>Asphodelus</i> L.	Lifante, 1996; Kosenko & Sventorzhetskaya, 1999	Obeso, 1992; Kubitzki, 1998a
		<i>Hemerocallis</i> L.	Takahashi, 1980; Xiong et al., 1998	Hotta et al., 1985; Kubitzki, 1998a
		<i>H. fulva</i> (L.) L. (Fig. 5A–C) <i>Xeronema</i> Brongn. & Gris	China, Yunnan, <i>S. D. Zhang et al. APE-LY-038</i> (KUN, living collection from KBC) Cranwell, 1953	Wardle, 1991; Chase et al., 2000
Arecaceae	183 (3)	<i>Calamus</i> L.	Sowunmi, 1972; Zhang & Liu, 1983; Ferguson & Harley, 1993	Essig, 1973; Henderson, 1986; Kubitzki, 1998b
		<i>C. nambariensis</i> Becc. (Fig. 5D–F)	China, Yunnan, <i>S. Y. Chen et al. 14369</i> (KUN)	
		<i>Euterpe</i> Mart. <i>Nypa</i> Steek	Sowunmi, 1972; Henderson & Galeano, 1996 Sowunmi, 1972; Harley & Baker, 2001	Essig, 1973; Henderson, 1986; Kubitzki, 1998b Essig, 1973; Henderson, 1986; Kubitzki, 1998b
DASYPOGONALES	4 (3)	<i>Kingia</i> R. Br.	Chanda & Ghosh, 1976	Kubitzki, 1998b
		<i>Calectasia</i> R. Br.	Chanda & Ghosh, 1976; Chanda et al., 1978	Kubitzki, 1998b
		<i>C. cyanea</i> R. Br. (Fig. 5G, H) <i>Dasypogon</i> R. Br.	Australia, Western Australia, <i>A. Morrison s.n.</i> (E) Chanda & Ghosh, 1976	Kubitzki, 1998b
COMMELINALES	40 (2)	<i>Cartonema</i> R. Br.	none	Kubitzki, 1998b
		<i>C. parviflorum</i> Hassk. (Fig. 5K, L)	Australia, Northern Territory, <i>R. Jensen 1837</i> (CANB)	
		<i>Murdannia</i> Royle <i>Anigozanthos</i> Labill.	Poole & Hunt, 1980; Yang et al., 2005 Simpson, 1983; Harley, 2004; Pierce & Simpson, 2009	Cook, 1990; Kubitzki, 1998b Keighery, 1980; Western Australian Herbarium, 1998 onwards
Haemodoraceae	14 (1)	<i>A. viridis</i> Endl. (Fig. 5I, J) <i>Hanguana</i> Blume	Australia, Western Australia, <i>A. Morrison s.n.</i> (E) Linder & Ferguson, 1985; Furness & Rudall, 1999	Maury, 1888; Cook, 1990; Kubitzki, 1998b
		<i>Philydrum</i> Banks ex Gaertn. <i>Pontederia</i> L.	Hamann, 1966; Simpson, 1985a Simpson, 1987	Cook, 1990; Kubitzki, 1998b Cook, 1990; Kubitzki, 1998b
		<i>Canna</i> L.	Skvarla & Rowley, 1970; Kress & Stone, 1982; Ludlow-Wiechers, 1982; Rowley & Skvarla, 1986	Cook, 1990; Kubitzki, 1998b

Appendix 1. Continued.

Taxonomic classification	Total # of genera per family (total # of genera sampled)	Taxon name, with species voucher	References and voucher information	
			References used for palynological data	References used for ecological data
Costaceae	6 (1)	<i>Costus</i> L.	Sharma, 1968; Furness, 1985; Liang, 1988; Mangaly & Nayar, 1990; Buchner & Weber, 2000 onwards	Kubitzki, 1998b
Heliconiaceae	1 (1)	<i>Heliconia</i> L. <i>H. subulata</i> Ruiz & Pav. (Fig. 6A–C) <i>Orchidantha</i> N. E. Br.	Erdtman, 1952; Kress et al., 1978; Stone et al., 1979; Kress & Stone, 1982, 1983 China, Yunnan, <i>L. Zhang Z107</i> (KUN, living collection from XTBC)	Kress, 1985a, 1985b; Kubitzki, 1998b
Lowiaceae	1 (1)		Long & Wen, 1997; Buchner & Weber, 2000 onwards	Kubitzki, 1998b; Sakai & Inoue, 1999
Marantaceae	31 (1)	<i>Maranta</i> L.	Erdtman, 1952	Kennedy, 2000
Musaceae	2 (1)	<i>Musa</i> L.	Erdtman, 1952; Sharma, 1968; Stroo, 2000	Kubitzki, 1998b
Strelitziaceae	3 (1)	<i>Strelitzia</i> Aiton	Hesse & Waha, 1983; Kronestedt-Robards & Rowley, 1989; Rowley et al., 1997; Furness & Rudall, 1999	Frost & Frost, 1981; Kubitzki, 1998b
Zingiberaceae	46 to 52 (1)	<i>Alpinia</i> Roxb.	Sharma, 1968; Liang, 1988; Mangaly & Nayar, 1990	Kubitzki, 1998b
POALES				
Anarthriaceae	3 (1)	<i>Anarthria</i> R. Br.	Ladd, 1977	Kubitzki, 1998b; Meney & Pate, 1999
Bromeliaceae	57 (2)	<i>Puya</i> Molina <i>Tillandsia</i> L.	Halbritter, 1992; Halbritter & Hesse, 1993; Stroo, 2000 Halbritter, 1992; Halbritter & Hesse, 1993; Albert et al., 2010	Ortiz Crespo, 1973; Kubitzki, 1998b Kubitzki, 1998b
Centrolepidaceae	3 (1)	<i>Aphelia</i> R. Br.	Chanda, 1966; Ladd, 1977	Kubitzki, 1998b
Cyperaceae	98 (2)	<i>Carex</i> L.	Van Wichelen et al., 1999; Nagels et al., 2009; Halbritter et al., 2010; Wronska-Pilarek et al., 2010	Cook, 1990; Kubitzki, 1998b
		<i>C. scaposa</i> C. B. Clarke (Fig. 6D–F) <i>Mapania</i> Aubl.	China, Yunnan, <i>S. D. Zhang et al. APE-LY-030</i> (KUN, living collection from KBC)	
Ecdeiocoleaceae	2 (1)	<i>Ecdeiocolea</i> F. Muell.	Van Wichelen et al., 1999; Simpson et al., 2003; Nagels et al., 2009	Kubitzki, 1998b
Eriocaulaceae	10 (1)	<i>Eriocaulon</i> L. <i>E. cristatum</i> Mart. (Fig. 6I, J)	Chanda, 1966; Chanda & Rowley, 1967; Ladd, 1977; Linder & Ferguson, 1985 Thanikaimoni, 1965; Furness, 1985, 1988; De Borges et al., 2009 China, Yunnan, <i>S. K. Wu et al. 3024</i> (KUN)	Cook, 1990; Kubitzki, 1998b Kubitzki, 1998b

Appendix 1. Continued.

Taxonomic classification	Total # of genera per family (total # of genera sampled)	Taxon name, with species voucher	References and voucher information	
			References used for palynological data	References used for ecological data
Flagellariaceae	1 (1)	<i>Flagellaria</i> L.	Chanda, 1966; Chanda & Rowley, 1967; Ladd, 1977; Linder & Ferguson, 1985	Linder, 1987; Kubitzki, 1998b
Joinvilleaceae	1 (1)	<i>Joinvillea</i> Gaudich. ex Brongn. & Gris	Chanda, 1966; Chanda & Rowley, 1967	Kubitzki, 1998b
Juncaceae	7 (2)	<i>Juncus</i> L.	Cranwell, 1953; Perveen, 1999; Buchner & Weber, 2000 onwards	Cook, 1990; Kubitzki, 1998b
		<i>J. sikkimensis</i> Hook. f. (Fig. 6C, H)	China, Yunnan, X. X. Zhu APE-LY-037 (KUN)	
Mayacaceae	1 (1)	<i>Luzula</i> DC.	Cranwell, 1953; Buchner & Weber, 2000 onwards	Cook, 1990; Kubitzki, 1998b
Poaceae	668 (2)	<i>Mayaca</i> Aubl. <i>Anomochloa</i> Brongn. <i>Oryza</i> L.	Zavada, 1983 Page, 1978; Michelangeli et al., 2003 Sharma, 1968; Page, 1978; Chaturvedi et al., 1998	Cook, 1990; Kubitzki, 1998b Cook, 1990; Kubitzki, 1998b Clayton & Renvoize, 1986; Judziewicz & Soderstrom, 1989; Givnish et al., 2010 Clayton & Renvoize, 1986; Givnish et al., 2010
		<i>Dendrocalamopsis beecheyana</i> (Munro) Keng f. var. <i>pubescens</i> (P. F. Li) Keng f. (Fig. 6K, L)	China, Yunnan, S. D. Zhang et al. APE-LY-22 (KUN, living collection from KBG)	
Rapateaceae	16 (1)	<i>Rapatea</i> Aubl.	Carlquist, 1961; Zavada, 1983; Tiemann, 1985	Kubitzki, 1998b
Restionaceae	58 (2)	<i>Elegia</i> L. <i>Baloskion</i> Raf. <i>Prionium</i> E. Mey. <i>Thurnia</i> Hook. f. <i>Sparganium</i> L. <i>Typha</i> L.	Chanda, 1966 Chanda, 1966; Briggs et al., 1999 Munro & Linder, 1997 Zavada, 1983 Nilsson et al., 1977; Zhang & Chen, 1984 Nilsson et al., 1977; Zhang & Chen, 1984; Perveen, 1999	Kubitzki, 1998b Kubitzki, 1998b Kubitzki, 1998b Cook, 1990; Kubitzki, 1998b Cook, 1990; Kubitzki, 1998b Cook, 1990; Kubitzki, 1998b Cook, 1990; Kubitzki, 1998b
Xyridaceae	5 (2)	<i>Abolboda</i> Bonpl. <i>Xyris</i> L.	Carlquist, 1960; Straka & Friedrich, 1984; Furness & Rudall, 1999; Campbell, 2012 Straka & Friedrich, 1984; Rudall & Sajo, 1999; Campbell, 2012	Cook, 1990; Kubitzki, 1998b; Oriani & Scatena, 2011 Cook, 1990; Kubitzki, 1998b
Outgroups AMBORELLALES				
Amborellaceae	1 (1)	<i>Amborella</i> Baill.	Sampson, 1993, 2000; Hesse, 2001	Kubitzki et al., 1993; Thien et al., 2003

Appendix 1. Continued.

Taxonomic classification	Total # of genera per family (total # of genera sampled)	Taxon name, with species voucher	References and voucher information	
			References used for palynological data	References used for ecological data
NYMPHAEALES				
Cabombaceae	2 (1)	<i>Cabomba</i> Aubl.	Walker, 1974, 1976; Osborn et al., 1991	Schneider & Jeter, 1982; Kubitzki et al., 1993
Nymphaeaceae	6 (1)	<i>Nymphaea</i> L.	Meyer, 1964; Gabarayeva & El-Chazaly, 1997; Sampson, 2000; Gabarayeva et al., 2001	Meeuse & Schneider, 1979; Cook, 1990; Kubitzki et al., 1993; Ervik & Knudson, 2003
AUSTROBAILEYALES				
Austrobaileyaceae	1 (1)	<i>Austrobaileya</i> C. T. White	Endress & Honegger, 1980; Zavada, 1984b; Sampson, 2000	Endress, 1990, 2001; Kubitzki et al., 1993
Schisandraceae	3 (2)	<i>Illicium</i> L. <i>Schisandra</i> Michx.	Lin, 1989; Liu & Yang, 1989; Takahashi, 1994; Sampson, 2000; Wang et al., 2010 Walker, 1974; Sampson, 2000; Sun, 2000; Wang et al., 2010	Thien et al., 1983, 2000; Kubitzki et al., 1993; Dieringer et al., 1999 Kubitzki et al., 1993; Thien et al., 2000; Yuan et al., 2007
CERATOPHYLLALES				
Ceratophyllaceae	1 (1)	<i>Ceratophyllum</i> L.	Díez et al., 1988; Takahashi, 1995	Cook, 1990; Kubitzki et al., 1993
CHLORANTHALES				
Chloranthaceae	4 (2)	<i>Ascarina</i> J. R. Forst. & G. Forst. <i>Chloranthus</i> Sw.	Kuprianova, 1967; Eklund et al., 2004 Kuprianova, 1967; Eklund et al., 2004	Kubitzki et al., 1993; Thien et al., 2000 Kubitzki et al., 1993; Thien et al., 2000
LAURALES				
Calycanthaceae	4 (1)	<i>Calycanthus</i> L.	Nicely, 1965; Li, 1990; Sampson, 2000; Staedler et al., 2009	Kubitzki et al., 1993
MAGNOLIALES				
Magnoliaceae	2 (2)	<i>Liriodendron</i> L. <i>Magnolia</i> L.	Canright, 1953; Agababian, 1972; Wei & Wu, 1993 Canright, 1953; Agababian, 1972; Sampson, 2000; Xu & Kirchoff, 2008	Kubitzki et al., 1993; Dieringer et al., 1999
CANELLALES				
Winteraceae	5 (1)	<i>Drimys</i> J. R. Forst. & G. Forst.	Walker, 1974; Zavada & Taylor, 1986; Sampson, 1995	Bernhardt & Thien, 1987; Kubitzki et al., 1993
PIPERALES				
Aristolochiaceae	5 to 8 (1)	<i>Asarum</i> L.	Mi & Yang, 1991; Sampson, 2000; Mulder, 2003; Perveen & Qaiser, 2008	Kubitzki et al., 1993; Kelly, 1997
Lactoridaceae	1 (1)	<i>Lactoris</i> Phil.	Zavada & Taylor, 1986; Sampson, 1995, 2000	Kubitzki et al., 1993
Saururaceae	5 (1)	<i>Saururus</i> L.	Sampson, 2000; Smith & Stockey, 2007	Cook, 1990; Kubitzki et al., 1993

Appendix 2. Comprehensive data matrix of pollen morphological and ecological characters analyzed in this study (see text and Table 1 for details). Taxon names are the same as those in Chase et al. (2006) throughout. One hundred twenty monocots and 16 outgroups are scored, and outgroup taxa are represented in italics. Inapplicable states are coded as “-” and unknown states as “?” Polymorphic states are enclosed in curly brackets.

Abolboda	00111020--00-0--022
Acanthochlamys	0100-2010?0021122??21
Acorus calamus	0100-1010100220-10122
Acorus gramineus	0100-1010100220-10122
Agapanthus	0100-{1,2}210000210-20?21
Agave	0100-12{1,2}0{0,1,2}00210-20?{2,4}0
Alania	0100-1110?00211120?21
Aletris	0100-11101002{0,1,2}0-{1,2}0121
Alisma	002110{0,1}431102211101{1,2}2
Allium	0100-{1,2}110{0,1}00220-{1,3,4}0120
Alpinia	00111020--0221100022
Alstroemeria	0100-1210{1,2}00220-{1,3,4}0?2{0,1,2}
Amborella	0{0,1}{0,1}1{0,1}0{0,1}02{0,1}02111701{1,2}2
Ananthria	0111{0,1}01102112212{1,3}011{1,2}
Anemarrhena	0100-2110?00210-20?20
Anigozanthos	0201-22{2,3}00101-0--050
Anomochloa	011110?10211221000?21
Aphelia	0111{0,1}0{0,1}10111221031?11
Aphyllanthes	0??11021-13022111??20
Arisaema	001110{0,1}0--022110-022
Arthropodium	0100-{1,2}110000210-2??21
Asarum	0211{0,1}0{1,2}{0,2,3,4}21{0,1}02{1,2}1{0,1,2}{1,2}0{0,1}22
Ascarina	011001{0,1}10100211020112
Asparagus	0100-{1,2}110{0,1}002{1,2}0-{1,2,3}012{0,1}
Asphodelus	0100-1210{0,1}002{1,2}0-{0,1,2}0121
Astelia	0100-{1,2}{0,1}10?002?11?0?2{1,2}
Austrobaileya	0100-11101002{1,2}0-{2,3}0122
Baloskion	011110?1011122??10112
Behnia	0100-?210?00210-2??2{1,2}
Blandfordia	0100-1110000220-3??5{1,2}
Borya	0100-{1,2}{0,1}10?00210-2??20
Brodiaea	0100-2210?00210-2??21
Butomus	0100-1110000210-20123
Cabomba	0100-2{1,2}10{1,2}00221210123
Calamus	0201-1{0,1}220002{1,2}{0,1}{1,2}{1,2,5}0122
Calectasia	0100-{2,3}{1,2}10200210-{1,2}0101
Calochortus	0100-2{1,2}{1,2}0000210-2??2{0,1,2}
Calycanthus	0200-{0,1}{1,2}{1,2}{0,2}1002{1,2}0-{1,2,3,5}0122
Campynema	0100-2110?00210-{1,2}0??1
Canna	00111020--00-0--0{4,5}2
Carex	1121{1,2}014{0,2}110221{0,1,2}{1,5}212{1,2}
Carludovica	01112{0,1}111?1?220-10122
Cartonema	0110-1210100210-6??21
Ceratophyllum	00111010--00-0--033
Chloranthus	0200-0{0,1}421{0,1}021{0,1}120122
Chlorophytum	0100-{1,2}110100220-1??{0,2}0
Chorigyne	0100-??10?00220-1?122
Clivia	0100-2210000210-20?{2,5}0
Convallaria	0100-{1,2}110000220-10122
Costus	0?211{0,1}3{1,4}30{1,3}01-0-0-0{2,5}2
Croomia	0100-1110100210-20121
Cyclanthus	0111{0,1}1{0,1}10010220-10122
Cymodocea	00-2--40--00-0--033
Cypripedium	0100-1110200220-{0,1}0021
Dasypogon	0100-1110000220-101{2,5}1
Dioscorea	0{1,2}01-{1,2,3}{0,1}{1,2,3}21002{1,2}0-{1,2,3,4}012{1,2}

Appendix 2. Continued.

Doryanthes	0100- $\{1,2\}$ 110200210-2?? $\{2,5\}$ 1
<i>Drimys</i>	111100 $\{0,1\}$ 10111210-2012 $\{1,2\}$
Ecdeiocolea	011110110211221210111
Elegia	011110110?11220-1?112
Epipactis	111110110 $\{0,1\}$ 10210-2?122
Eriocaulon	0??110 $\{0,1\}$ $\{1,2,3\}$?130221 $\{0,1\}$ $\{0,1,3\}$ 012 $\{1,2\}$
Euterpe	0100-2 $\{1,2\}$ 101002 $\{1,2\}$ 0- $\{1,2\}$ 0?2 $\{1,2\}$
Flagellaria	0111101101112212 $\{1,3\}$ 011 $\{1,2\}$
Freycinetia	0111 $\{0,1\}$ 1 $\{0,1\}$ 1001122 $\{0,1\}$ 0 $\{0,1\}$ 01 $\{4,6\}$ 2
Gymnostachys	0100-1110100220- $\{1,5\}$ 0122
Hanguana	001110 $\{0,1\}$ 0---00-0---022
Heliconia	0111 $\{0,1\}$ 020---00-0---0 $\{4,5\}$ 2
Hemerocallis	0100- $\{2,3\}$ $\{2,3\}$ 10000210-20121
Herreria	0100-?110?00210-20??2
Hypoxis	0100- $\{1,2\}$ 110100210-20?2 $\{1,2\}$
<i>Illicium</i>	0211 $\{0,1\}$ 01321 $\{0,4\}$ 0210-20121
Ixiolirion	0100-2 $\{1,2\}$ 10200210-20?20
Japonolirion	0100-1010?00200--01?2
Joinvillea	011110110111221011011
Juncus	111110 $\{0,1\}$ 101102210 $\{0,1\}$?? $\{1,2\}$ $\{1,2\}$
Kingia	0100-1 $\{1,2\}$ 10000220- $\{0,1\}$ 01 $\{2,5\}$ 1
<i>Lactoris</i>	11 $\{0,1\}$ 0 $\{0,1\}$ 0 $\{0,1\}$ 0 $\{0,1\}$ 101 $\{0,1\}$ 0210- $\{1,3\}$ $\{0,1\}$ 111
Lanaria	0100-1 $\{0,1\}$ 10000220-10121
Lilium	01 $\{0,1\}$ 0- $\{1,2\}$ $\{2,3\}$ $\{1,2,3\}$ 01 $\{0,1\}$ 0210-20121
<i>Liriodendron</i>	0100- $\{1,2\}$ $\{1,2\}$ 101002 $\{1,2\}$ 0- $\{1,2,3\}$ 012 $\{1,2\}$
Luzula	1111101101102210 $\{0,1\}$?? $\{1,2\}$ $\{1,2\}$
Luzuriaga	0100-1 $\{0,1\}$ 10100210-2??02
<i>Magnolia</i>	0100- $\{1,2\}$ $\{1,2\}$ 1010022 $\{0,1\}$ 0 $\{1,3\}$ $\{0,1,2\}$ 12 $\{1,2\}$
Mapania	111110 $\{0,1\}$ 101112 $\{1,2\}$ 0 $\{0,1\}$ 0 $\{1,2,5\}$ 0122
Maranta	001110?0---00-0---022
Mayaca	0100-1?101002 $\{0,1\}$ 0-20122
Murdannia	0100-2110100221 $\{0,2\}$ 10121
Musa	001110 $\{2,3\}$ 0---00-0---0 $\{4,5\}$ 2
Nartheceium	0100-1 $\{0,1\}$ 102002 $\{1,2\}$ 0- $\{1,2\}$ 0122
Neuwiedia	0100-1010200210-20122
<i>Nymphaea</i>	0 $\{1,2\}$ 0 $\{0,1\}$ 0 $\{0,1\}$ 0 $\{0,1\}$ 1 $\{1,2\}$ 12 $\{0,1\}$ 0 $\{0,2\}$ 0221 $\{0,1,2\}$ 0 $\{0,2\}$ 0 $\{0,1,2\}$ 122
Nypa	0211101120202 $\{1,2\}$ 11 $\{1,2\}$ 0122
Orchidantha	01012030---00-0---022
Orontium	0100- $\{1,2\}$ 210100220- $\{1,5\}$ 0122
Oryza	011110110211211 $\{0,1\}$ 0 $\{0,6\}$ 0?11
Pandanus	0111 $\{1,2\}$ 0 $\{0,1\}$ 1001 $\{0,1\}$ 1 $\{1,2\}$ 1 $\{1,2\}$ 0 $\{0,1\}$ 0 $\{0,1,2\}$ 0 $\{0,1,2,5\}$ 0 $\{0,2\}$ 0 $\{0,1\}$ 1 $\{1,2,4\}$ 2
Petermannia	0100-2110?0022115??22
Petrosavia	0100-2 $\{0,1\}$ 10100210- $\{1,2\}$ 0? $\{0,2\}$ 1 $\{1,2\}$
Philesia	00110020---021110??5 $\{1,2\}$
Philydrum	1100-1110000210-20122
Pleea	0201-1 $\{0,1\}$ 2??00210-20121
Pontederia	0100-21 $\{2,3\}$ 0 $\{0,2\}$ 000220- $\{0,3,5\}$ 0123
Potamogeton	$\{0,1\}$ 011 $\{0,1\}$ 0 $\{0,1\}$ 0---0211120113
Pronium	11111001011022100??12
Puya	0100-1210000210-201 $\{4,5\}$ 1
Rapatea	0211101121202 $\{1,2\}$ 0- $\{1,2\}$ 012 $\{1,2\}$
Rhipogonum	0100- $\{1,2\}$ 110?0021 $\{0,1\}$ 120122
Sagittaria	002110 $\{0,1\}$ 43110221 $\{0,1\}$ 101 $\{1,2\}$ 3
<i>Saururus</i>	0100-2010100221010122
Schelhammera	0100- $\{1,2\}$ 210?002????0?22
<i>Schisandra</i>	011100 $\{0,1\}$ 3 $\{3,4\}$ 0 $\{0,2\}$ 1 $\{0,4\}$ 0210-20121
Scilla	0100- $\{1,2\}$ 1100002 $\{1,2\}$ 0- $\{1,2\}$ 0121
Sisyrinchium	0100-2 $\{1,2\}$ 10000210-20121
Smilax	001110 $\{0,1\}$ 0---02 $\{0,2\}$ 1131022
Sparganium	011110110110210-20?12

Appendix 2. Continued.	
Sphaeradenia	01{0,1}{0,1}{0,1}21100{0,1}02{1,2}0-{1,2}012{1,2}
Stemona	0100-1{0,1}101002{0,1,2}0-{0,1,2,3,5}{0,1,2}12{0,1}
Strelitzia	00111030---00-0---052
Tacca	0100-{1,2}1101002{1,2}0-{2,3}01{0,2}2
Talbotia	0100-1010200220-301?2
Tecophilaea	0100-1110200220-301?1
Thurnia	111110010110211160?12
Tillandsia	0100-{1,2}{1,2}1{0,1}{1,2}002{1,2}0-{1,2}01{2,5}{0,1}
Tofieldia	0201-1{0,1}2210021{0,1}{0,2}{1,2}012{1,2}
Trichopus	0100-10101002211???02
Triglochin	001110{0,1}0---0210-20112
Trillium	001110{0,1}0---0{0,2}{0,1}0-30{0,1}2{1,2}
Typha	{0,1}11110{0,1}10110210-20?12
Uvularia	0100-{1,2}1{1,2}0200211{0,1}10?2{1,2}
Vallisneria	00111030---00-0---033
Veratrum	0100-{1,2}110200210-2???22
Xanthorrhoea	0100-{1,2}110?00210-201{2,5}1
Xeronema	0100-1110000210-2?1{2,5}0
Xyris	0100-11{1,2}0{1,2}00210-2???2{1,2}
Zostera	00-2---40---00-0---033

Appendix 3. Democratic data matrix of pollen morphological and ecological characters analyzed in this study (see text and Table 1 for details). Taxon names are the same as those in Chase et al. (2006) throughout. One hundred twenty monocots and 16 outgroups are scored, and outgroup taxa are represented in italics. Inapplicable states are coded as “-” and unknown states as “?”.

Abolboda	00111020---00-0---0
Acanthochlamys	0100-2010?0021122??
Acorus_calamus	0100-1010100220-101
Acorus_gramineus	0100-1010100220-101
Agapanthus	0100-2210000210-20?
Agave	0100-1210100210-20?
Alania	0100-1110?00211120?
Aletris	0100-1110100210-201
Alisma	0021100431102211101
Allium	0100-1110100220-401
Alpinia	00111020--02211000
Alstroemeria	0100-1210100220-30?
Amborella	0111000102102111701
Anarthria	0111101102112212301
Anemarrhena	0100-2110?00210-20?
Anigozanthos	0200-22200101-0--0
Anomochloa	011110?10211221000?
Aphelia	011110010111221031?
Aphyllanthes	0??11021-13022111??
Arisaema	00111000--022110-0
Arthropodium	0100-2110000210-2??
Asarum	0211102321002112201
Ascarina	0110010101002110201
Asparagus	0100-2110100220-101
Asphodelus	0100-1210100220-101
Astelia	0100-1010?002?11?0?
Austrobaileya	0100-1110100210-201
Baloskion	011110?1011122??101
Behnia	0100-?210?00210-2??
Blandfordia	0100-1110000220-3??
Borya	0100-2110?00210-2??
Brodiaea	0100-2210?00210-2??
Butomus	0100-1110000210-201
Cabomba	0100-22102002212101
Calamus	0201-1122000210-201
Calectasia	0100-2210200210-201
Calochortus	0100-2110000210-2??
Calycanthus	0200-0122100210-201
Campynema	0100-2110?00210-20?
Canna	00111020---00-0---0
Carex	1121101401102210121
Carludovica	011120111?1?220-101
Cartonema	0110-1210100210-6??
Ceratophyllum	00111010--00-0---0
Chloranthus	0200-00421002101201
Chlorophytum	0100-2110100220-1??
Chorigyne	0100-??10?00220-1?1
Clivia	0100-2210000210-20?
Convallaria	0100-2110000220-101
Costus	0?21103430101-0-0-0
Croomia	0100-1110100210-201
Cyclanthus	011101110010220-101
Cymodocea	00-2--40--00-0---0
Cypripedium	0100-1110200220-000

Appendix 3. Continued.

Dasypogon	0100-1110000220-101
Dioscorea	0200-1122100220-101
Doryanthes	0100-2110200210-2??
Drimys	111100110111210-201
Ecdeiocolea	0111101102112212101
Elegia	011110110?11220-1?1
Epipactis	111110110010210-2?1
Eriocaulon	0??11011?1302211101
Euterpe	0100-2110100220-10?
Flagellaria	0111101101112212301
Freycinetia	011101010011220-101
Gymnostachys	0100-1110100220-101
Hanguana	00111000---00-0---0
Heliconia	01111020--00-0---0
Hemerocallis	0100-3310000210-201
Herreria	0100-?110?00210-20?
Hypoxis	0100-2110100210-20?
Illicium	021110132100210-201
Ixiolirion	0100-2110200210-20?
Japonolirion	0100-1010?00200--01
Joinvillea	0111101101112210110
Juncus	11111001011022101??
Kingia	0100-1210000220-101
Lactoris	111110110100210-311
Lanaria	0100-1110000220-101
Lilium	0100-2210100210-201
Liriodendron	0100-2210100220-101
Luzula	11111011011022101??
Luzuriaga	0100-1110100210-2??
Magnolia	0100-2210100220-101
Mapania	1111100101112210101
Maranta	001110?0--00-0---0
Mayaca	0100-1?101002-0-201
Murdannia	0100-21101002212101
Musa	00111020--00-0---0
Nartheccium	0100-1010200210-201
Neuwiedia	0100-1010200210-201
Nymphaea	0211101120202212011
Nypa	0211101120202211101
Orchidantha	01012030--00-0---0
Orontium	0100-2210100220-101
Oryza	011110110211211060?
Pandanus	0111200100101-0--0
Petermannia	0100-2110?0022115??
Petrosavia	0100-2010100210-20?
Philesia	00110020--021110??
Philydrum	1100-1110000210-201
Pleea	0200-102??00210-201
Pontederia	0100-2122000220-301
Potamogeton	00111000--02111201
Prionium	11111001011022100??
Puya	0100-1210000210-201
Rapatea	021110112120210-201
Rhipogonum	0100-1110?00210-201
Sagittaria	0021100431102211101
Saururus	0100-20101002210101
Schelhammera	0100-2210?002????0?
Schisandra	011100142140210-201
Scilla	0100-2110000210-201
Sisyrinchium	0100-2110000210-201

Appendix 3. Continued.

Smilax	00111000---0200--10
Sparganium	011110110110210-20?
Sphaeradenia	0101-2110000220-101
Stemona	0100-1110100200--11
Strelitzia	00111030---00-0---0
Tacca	0100-2110100220-301
Talbotia	0100-1010200220-301
Tecophilaea	0100-1110200220-301
Thurnia	111110010110211160?
Tillandsia	0100-1110100210-201
Tofieldia	0200-1022100210-201
Trichopus	0100-10101002211???
Triglochin	00111000---0210-201
Trillium	00111010---00-0---0
Typha	111110110110210-20?
Uvularia	0100-1110200211110?
Vallisneria	00111030---00-0---0
Veratrum	0100-2110200210-2??
Xanthorrhoea	0100-1110?00210-201
Xeronema	0100-1110000210-2?1
Xyris	0100-1110200210-2??
Zostera	00-2--40---00-0---0

Appendix 4. Data matrix of pollen morphological and ecological characters used in analyses of correlated evolution (see text and Table 1 for details). Taxon names used are the same as those in Chase et al. (2006) throughout. One hundred twenty monocots and 16 outgroups are scored, and outgroup taxa are represented in italics. Unknown states are coded as “?”.

Abolboda	00000010
Acanthochlamys	11011000
Acorus_calamus	11111011
Acorus_gramineus	11111011
Agapanthus	11011000
Agave	11011000
Alania	11011000
Aletris	11011000
Alisma	11111011
Allium	11111000
Alpinia	11111000
Alstroemeria	11111000
Amborella	11111000
Anarthria	11111000
Anemarrhena	11011000
Anigozanthos	10000000
Anomochloa	11111000
Aphelia	11110100
Aphyllanthes	11111000
Arisaema	11111000
Arthropodium	11011000
Asarum	11011000
Ascarina	11011000
Asparagus	11011000
Asphodelus	11011000
Astelia	11?11000
Austrobaileya	11011000
Baloskion	11111010
Behnia	11011000
Blandfordia	11111000
Borya	11011000
Brodiaea	11011000
Butomus	11011011
Cabomba	11111011
Calamus	11011000
Calectasia	11011000
Calochortus	11011000
Calycanthus	11011000
Campynema	11011000
Canna	00000010
Carex	11111010
Carludovica	11111000
Cartonema	11011000
Ceratophyllum	00000011
Chloranthus	11011000
Chlorophytum	11111000
Chorigyne	11111000
Clivia	11011000
Convallaria	11111000
Costus	10000010
Croomia	11011000
Cyclanthus	11111010
Cymodocea	00000011

Appendix 4. Continued.		Appendix 4. Continued.	
Cypripedium	11111000	Rhipogonum	11011000
Dasypogon	11111000	Sagittaria	11111011
Dioscorea	11111000	<i>Saururus</i>	11111010
Doryanthes	11011000	Schelhammera	11?11000
Drimys	11011000	Schisandra	11011000
Ecdeiocolea	11111000	Scilla	11011000
Elegia	1111??00	Sisyrinchium	11011000
Epipactis	1101??00	Smilax	10010100
Eriocaulon	11111010	Sparganium	11011011
Euterpe	11111000	Sphaeradenia	11111000
Flagellaria	11111000	Stemona	11011000
Freycinetia	11111000	Strelitzia	00000010
Gymnostachys	11111000	Tacca	11111000
Hanguana	00000011	Talbotia	11111000
Heliconia	00000010	Tecophilaea	11111000
Hemerocallis	11011000	Thurnia	11011011
Herreria	11011000	Tillandsia	11011000
Hypoxis	11011010	Tofieldia	11011000
<i>Illicium</i>	11011000	Trichopus	11?11010
Ixiolirion	11011000	Triglochin	11011010
Japonolirion	10011010	Trillium	00000000
Joinvillea	11110100	Typha	11011011
Juncus	1111??10	Uvularia	11111000
Kingia	11111000	Vallisneria	00000011
Lactoris	11110100	Veratrum	11011000
Lanaria	11111000	Xanthorrhoea	11011000
Lilium	11011000	Xeronema	11011000
<i>Liriodendron</i>	11111000	Xyris	11011010
Luzula	1111??00	Zostera	00000011
Luzuriaga	11011000		
<i>Magnolia</i>	11111000		
Mapania	11111000		
Maranta	00000010		
Mayaca	10011011		
Murdannia	11111010		
Musa	00000010		
Narthecium	11011010		
Neuwiedia	11011000		
<i>Nymphaea</i>	11110111		
Nypa	11111000		
Orchidantha	00000010		
Orontium	11111011		
Oryza	11011010		
Pandanus	11000000		
Petermannia	11111000		
Petrosavia	11011000		
Philesia	11111000		
Philydrum	11011010		
Plea	11011000		
Pontederia	11111011		
Potamogeton	11011011		
Pronium	1111??10		
Puya	11011000		
Rapatea	11011000		

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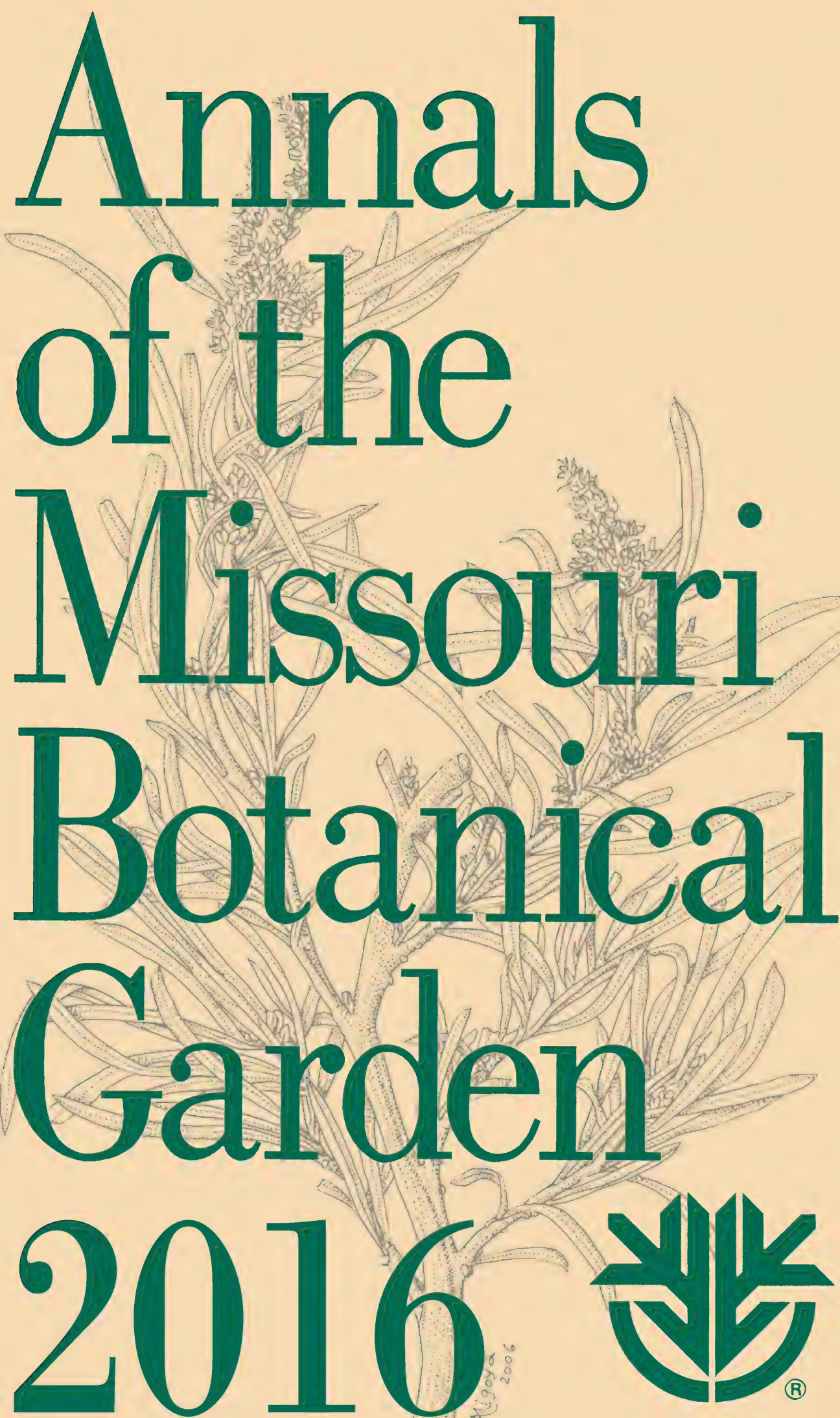
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Cover illustration. *Amaranthus brownii* Christoph. & Caum., drawn by Alejandra Migoya.



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A TAXONOMIC REVISION OF
PHILIPPINE *MUSSAENDA*
(RUBIACEAE, MUSSAENDEAE)¹

Grecebio Jonathan D. Alejandro,^{2,3} Ulrich Meve,³
and Sigrid Liede-Schumann³

ABSTRACT

The Philippine taxa of *Mussaenda* Burm. ex L. (Rubiaceae, Ixoroideae, Mussaendeae) are revised here, based on field observations and study of herbarium specimens. Twenty-four species and four varieties are recognized, with three new species and one new variety. In the Philippines, *M. grandibracteata* Alejandro is described from the province of Occidental Mindoro, *M. liedae* Alejandro from Palawan, and *M. milleri* Elmer ex Alejandro from Nueva Ecija; *M. philippica* A. Rich var. *pubescens* Alejandro is described from Davao Oriental. A lectotype is newly designated for *M. benguetensis* Elmer, and the invalid name *M. milleri* is validated herein. *Mussaenda macrophylla* Wall. var. *grandisepala* (Jayaw.) Alejandro has new status for its rank as variety rather than form, and the epithet *grandisepala* is lectotypified. Subsequent lectotypifications are designated for *M. scandens* Elmer and *M. vidalii* Elmer. The morphology of Philippine *Mussaenda* is compared with Asian and African *Mussaenda* and is distinguished from other genera of Mussaendeae by its reduplicate-valvate corolla aestivation. The forms of trichomes and morphology of the calyx and corolla are valuable characters for species recognition. Variation of trichomes inside the corolla exists between the short- and long-styled flower morphs and is an important character in recognizing some Philippine *Mussaenda*.

Key words: IUCN Red List, Ixoroideae, *Mussaenda*, Mussaendeae, Philippines, Rubiaceae, subsequent lectotypification.

Mussaenda Burm. ex L. (Rubiaceae, Ixoroideae, Mussaendeae) is a widely accepted genus ranging from shrubs to small trees, scandent shrubs, lianas, or rarely, suffrutices. The genus as currently delimited (sensu Alejandro et al., 2005) is mostly paleotropical, comprising ca. 135 species distributed throughout

the moist tropics of Asia with ca. 100 species and in Africa with ca. 35 species (Bridson & Verdcourt, 1988). *Mussaenda* is the most widespread and species-rich genus of the seven genera within the Mussaendeae (Bremer & Thulin, 1998; Bremer et al., 1999; Rova et al., 2002), with the other six being

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Bremeria Razafim. & Alejandro (28 species, including *B. pervillei* (Wernham) Razafim. & Alejandro from Madagascar), *Heinsia* DC. (four or five species, including *H. crinita* (Afzel.) G. Taylor), *Landiopsis* Capuron ex Bosser (monotypic), *Neomussaenda* Tange (two species), *Pseudomussaenda* Wernham (four or five species), and *Schizomussaenda* H. L. Li (two species) (Alejandro et al., 2005). *Mussaenda* is characterized by enlarged calyx lobes or calycophylls (sensu Delprete, 1996), indehiscent fruits, containing numerous small, reticulate seeds. Among Mussaendeae, *Mussaenda* is distinguished by its reduplicate-valvate corolla aestivation (Alejandro et al., 2005; 2008). Both morphology (Puff et al., 1993) and molecular data (ITS and *trnT-F*) (Alejandro et al., 2005) support a sister relationship between *Mussaenda* and *Pseudomussaenda*, but the latter is distinct by its induplicate-valvate aestivation and capsular fruits (Wernham, 1916). Although there is no morphological synapomorphy for the *Mussaenda*–*Pseudomussaenda* group, these taxa are characterized by smaller corollas less than 5 cm, compared to its sister *Bremeria*–*Landiopsis* group, with larger corollas greater than 5 cm (Alejandro et al., 2005).

Many species of *Mussaenda* are cultivated in botanical gardens all over the world because of their resilience and long blooming period throughout almost the entire year. The discovery of *M. philippica* A. Rich var. *aurorae* Sulit (with all five calyx lobes enlarged) then crossed with the African *M. erythrophylla* Schumach. & Thonn., which led to the development and propagation of ca. 20 Philippine hybrids (Rosario, 1998) that are known for their splendid and iridescent, enlarged calyx lobes.

Merrill (1923) enumerated 18 species of *Mussaenda* native to the Philippines. Later, Jayaweera (1964) published a herbarium-based study that included 19 species, one variety, and one form. For species recognition, Jayaweera emphasized the number and distribution of stipule colleters and the size and number of perforations on the inner tangential walls of the seed exotesta cells. However, these characters are labile, varying even within a species. Recent evaluation showed that other features such as the vegetative character of the external indumentum and the reproductive character of corolla trichomes mentioned by Jayaweera (1964) to be inaccurate. The Philippine *Mussaenda* comprise species of trees or shrubs, rarely scandent, that thrive in a variety of habitats such as coastal scrubs and thickets, disturbed roadsides, ravines, riversides and stream banks, secondary and primary forests, savanna, and lowland or montane forests. Additional taxonomically useful characters have proved to be the corolla

indumentum of both the short- and long-styled morphs of the flower, seed exotesta cells, and pollen.

METHODS

A taxonomic revision of the Philippine *Mussaenda* is presented herein as part of an ongoing project on Philippine Rubiaceae (Alejandro & Liede, 2003). This was based on the examination of over 600 herbarium specimens from A, BM, BR, L, MO, NY, P, PNH, US, and WAG (abbreviations after Holmgren et al., 1990), and on field studies (2002, 2003, 2010) on 20 of the 28 taxa of Philippine *Mussaenda* recognized here (cf. Appendices 1 and 2). Measurements of flowers and fruits are based mostly on collections preserved in 70% ethanol (Radford et al., 1973). For the few species for which no liquid material was available, measurements are based on rehydrated structures, using distilled water of Pohl's solution (Pohl, 1965).

Seeds were placed in an ultrasonic cleaner (30 min.; distilled water) in order to remove the outer tangential walls of exotesta cells. Pollen grains obtained from our collections were prepared by the acetolysis method (Erdtman, 1943). For SEM (Philips XL-30; Philips, Amsterdam, The Netherlands) investigations, prepared specimens were dehydrated in an ethanol series and formaldehyde dimethyl acetal (FDA) and subsequently critical point-dried. Dried samples were mounted on aluminum stubs, which were covered with polyvinyl acetate (PVA) glue and then sputter-coated with gold.

The data for each species were initially gathered against a character list, which encompassed over 200 characters used to generate a natural language description in DELTA format (Dallwitz et al., 1999) and then edited. In the taxonomic treatment, the summarized morphological characters of *Mussaenda* are based exclusively on the Philippine species. The local names, gathered through interviews and labels from herbarium specimens, are given for each species with the standard abbreviation of local dialects (Madulid, 2001) in parentheses.

MORPHOLOGY OF THE PHILIPPINE MUSSAENDA

HABIT

Plants of *Mussaenda* are terrestrial, woody, and usually shrubs (erect or scandent) to small- or medium-sized trees, but rarely true lianas and suffrutices (Asian *M. uniflora* Wall. ex G. Don and *M. parva* Wall. ex G. Don). The Philippine species are at the most 8 m high (e.g., *M. benguetensis* Elmer, *M. multibracteata* Merr., and *M. pinatubensis* Elmer), while some African *Mussaenda* can reach 9 m in

height or more (e.g., *M. elegans* Schumach. & Thonn., *M. microdonta* Wernham, and *M. monticola* K. Krause). Three Philippine species tend toward becoming scandent or climbing shrubs (*M. macrophylla* Wall. var. *brevipilosa* Jayaw., *M. scandens* Elmer, and *M. vidalii* Elmer). Scandent or climbing shrubs are also found in *Heinsia* and *Pseudomussaenda*, whereas other Mussaendeae genera (*Bremeria*, *Landiopsis*, *Neomussaenda*, and *Schizomussaenda*) are typically erect shrubs or trees. The stems of *Mussaenda* are generally pubescent when young, becoming glabrescent. Lateral branches are more or less plagiotropic (except in lianas and suffrutices); mature stems are more or less cylindrical, lenticellate, and their bark can be easily peeled. Young branches are somewhat flattened and usually covered with a whitish or brownish to red indumentum. The external indumentum, which extends to the stipules and inflorescences, is of the cylindrical type, pluricellular, with few (< 12) or many (> 12) cells (cf. Robbrecht, 1988: fig. 19F). The various types of indumentum are useful in recognizing some Philippine species of which more than half are hirsute (e.g., *M. anisophylla* S. Vidal and *M. vidalii*). Indument varies from pilose (*M. chlorantha* Merr., *M. nervosa* Elmer, and *M. palawanensis* Merr.) or glabrous to puberulous (*M. philippica* var. *philippica*, *M. pinatubensis*, *M. scandens*, and *M. grandibracteata* Alejandro), and rarely velvety (only in *M. grandifolia* Elmer). The reddish brown indumentum on both vegetative and reproductive parts of *M. milleri* Elmer ex Alejandro is a diagnostic feature of the species.

LEAVES

Mussaenda leaves are opposite and decussate and generally coriaceous to membranaceous. Leaf arrangement seems consistent within a species, although leaves may show a trend toward anisophyly. All Philippine species are usually petiolate, though they may rarely be sessile, with the petiole varying from 0.3 to 8 cm. The petioles are usually hairy except for those in *M. grandibracteata* and occasionally in *M. macrophylla* var. *brevipilosa*. Leaf blades vary from ovate, or elliptic, rarely obovate to orbicular. In the Philippine species, leaf blades range from small to relatively large (3.5–34 × 1.8–16.5 cm). Most species possess medium-sized blades varying from 10 to 25 cm (e.g., *M. acuminatissima* Merr., *M. attenuifolia* Elmer, and *M. ustii* Alejandro). Larger leaf blades reaching lengths to 34 cm are found in *M. anisophylla*, *M. grandifolia*, *M. lanata* C. B. Rob., and *M. multibracteata*, while lengths of less than 15 cm occur in *M. benguetensis*, *M. milleri*, *M. scandens*, and *M. pinatubensis*. Small leaf blades (3.5–12 ×

1.8–4 cm) distinguish *M. pinatubensis*. Leaf blades are usually hairy on both sides, especially along the midrib and secondary nerves abaxially. Typically, terminal leaves supporting the inflorescence are smaller, with a denser indumentum, and often subsessile. Leaf apices are usually acute, or acuminate to subcaudate, the acumen extending from 0.5 to 1.5 cm. Three species show a rare conduplicate apex (*M. nervosa*, *M. philippica* var. *pubescens* Alejandro, and *M. scandens*). Leaf bases are usually cuneate or attenuate but may vary from obtuse to acute. The midrib and secondary veins are very prominent abaxially and usually prominulous adaxially. Only *M. nervosa* has a blade midrib and secondary veins that are distinctly sunken adaxially. The secondary veins are generally brochidodromous. Domatia, almost universally present in woody Rubiaceae, are entirely lacking in *Mussaenda* as well as in the rest of Mussaendeae.

STIPULES

The stipules of Mussaendeae are interpetiolar, triangular, typically bifid (halfway to almost near the base), rarely entire, and opposite pairs are sometimes basally fused, forming a ring around the node. In the Philippine species of *Mussaenda*, bifurcation of stipules is at the most slightly diverging or rarely prominently diverging as distinctively exhibited by *M. benguetensis*. Both surfaces of the stipules are usually more or less densely indumented. The distribution of trichomes adaxially varies from all over the whole surface to only restricted to the base and/or apex, leaving the middle portion glabrous (e.g., *M. benguetensis*, *M. lanata*, and *M. vidalii*).

COLLETTERS

Mussaendeae colleters are present on the adaxial surfaces of both stipules and calyx lobes. The stipular colleters vary, occurring either in groups of two (Fig. 1A) or in a continuous band at the base (Fig. 1B). In Philippine *Mussaenda*, paired groups of colleters predominate, but variation sometimes exists even on the same branch. Colleters are usually found between sinuses of the calyx lobes as in many Gentianales. In the Philippine species, calyx colleters are small and typically solitary or in a group of two to five, rarely occurring in a row at the base of calyx lobes (*M. benguetensis*). Colleter number is not a reliable character because this may vary even among individual lobes of the same flower, as is the case in other Mussaendeae. In some *Bremeria* species, the colleters are distributed along the calyx margins

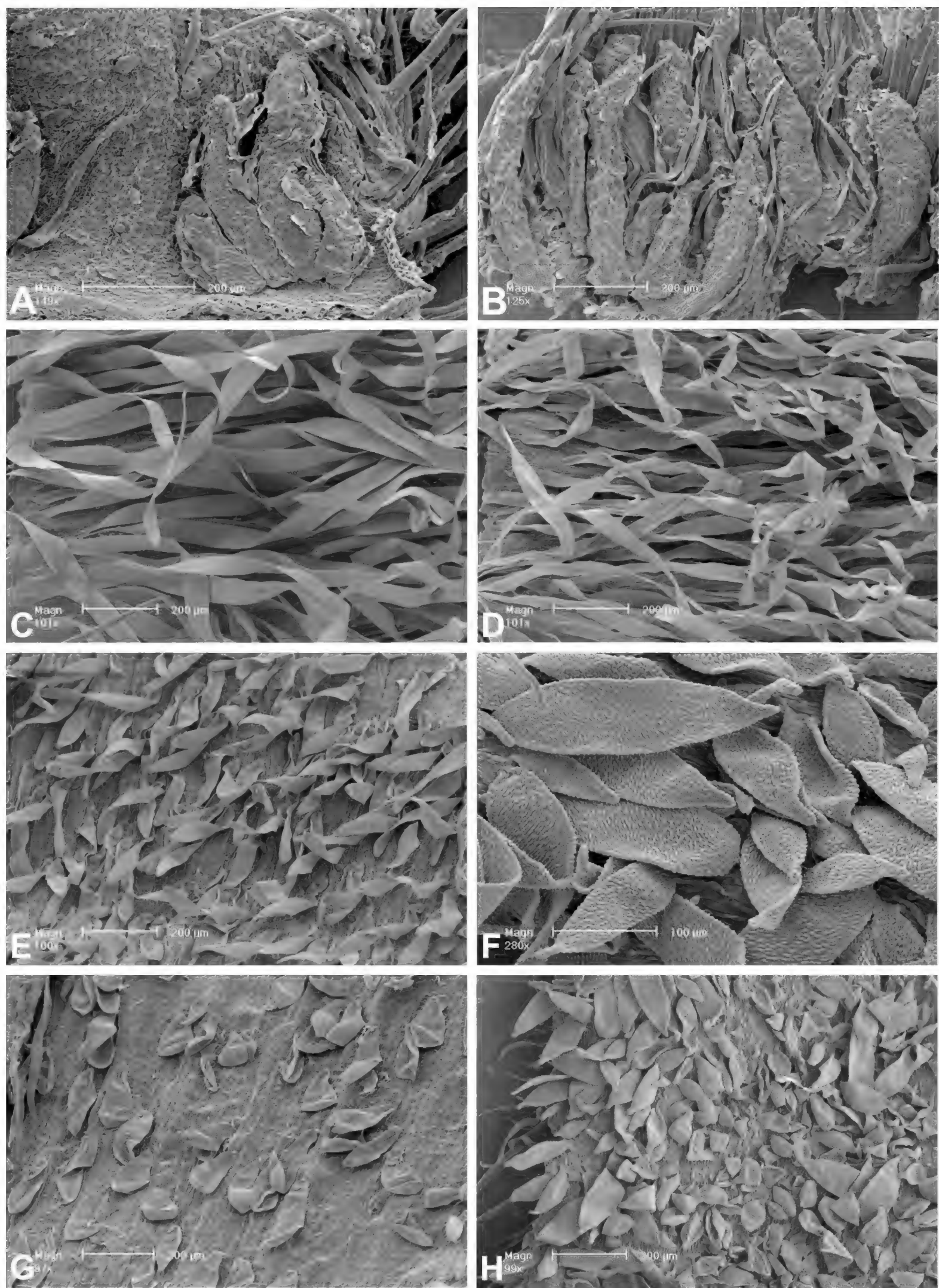


Figure 1. A, B. Distribution of colleters on the adaxial side of stipules in *Mussaenda* Burm. ex L. —A. *Mussaenda benguetensis* Elmer. Colleters in groups of two, with one isolated group shown. —B. *Mussaenda scandens* Elmer. Colleters in continuous band. C–H. Variations of unicellular trichomes inside the corolla. —C. *Mussaenda lideae* Alejandro. Long, ribbon-like, unstriate trichomes densely distributed inside the corolla in short-styled flower morphs. —D. *Mussaenda albiflora* Merr. Long, ribbon-like, unstriate trichomes densely distributed inside the corolla in short-styled flower morphs. —E. *Mussaenda albiflora* Merr. Ribbon-like trichomes sparsely distributed in long-styled flower morphs. —F. *Mussaenda benguetensis* Elmer.

extending to almost half of the lobes (e.g., *B. vestita* (Baker) Razafim. & Alejandro).

INFLORESCENCES

The inflorescences of *Mussaenda* are typically terminal but may be displaced to pseudoaxillary (Robbrecht, 1988). These are cymose corymbs, congested or spreading, with few to many flowers, or rarely reduced to a single flower (*M. uniflora*). Based on the four types of development and specialization of pseudanthia recognized by Claßen (1984), the calycophyllous type characterized by the presence of enlarged calyx lobes occurs in *Mussaenda*. The inflorescence axes of both *Mussaenda* and *Pseudomussaenda* are characterized by a regular, sympodial-dichasial branching of their ultimate elements (Puff et al., 1993). Indumentum is approximately as dense as the young twigs and relatively constant within a species. In Philippine *Mussaenda*, the inflorescence axes may vary from being densely covered with trichomes to sparsely so (*M. liedae* Alejandro and *M. viridiflora* Alejandro), or are almost glabrous (*M. grandibracteata*, *M. philippica* var. *philippica*, *M. pinatubensis*, and *M. scandens*). Small bracts are generally present on the inflorescence axes and flower pedicels. Bracts are opposite in arrangement, with linear or lanceolate to ovate shapes and acuminate or gradually pointed tips, and are normally caducous. In Philippine *Mussaenda*, bracts are usually entire, or trilobed with the lateral lobes always shorter. There are some reported 3- to 5-lobed bracts in African *Mussaenda* (e.g., *M. erythrophylla*). Jayaweera (1963) considered the bracts insignificant for differentiation among the Asian *Mussaenda* species. However, the Philippine species vary in the degree of indumentum and bract size and this may be useful for recognizing some Philippine species. The abaxial bract surface is usually glabrous or sparsely to densely covered with trichomes, or with a tuft of trichomes at the base (*M. multibracteata*), or with a few scattered trichomes only at the base (*M. nervosa*). One species, *M. grandibracteata*, can be recognized by its large bracts (7–13 × 2.5–5 mm).

FLOWERS

The flowers of *Mussaenda* are actinomorphic and usually 5-merous, although 6-merous flowers rarely

occur (*M. benguetensis* and *M. palawanensis*). Among Philippine *Mussaenda*, only *M. benguetensis* and *M. viridiflora* emit a sweet scent similar to that of *Gardenia* J. Ellis. Bridson and Verdcourt (1988) recorded some sweet-scented species in African *Mussaenda* (e.g., *M. arcuata* Poir. and *M. microdonta*) and Malagasy *Bremeria* (e.g., *B. erectiloba* (Wernham) Razafim. & Alejandro).

CALYX

The calyx tubes are typically cup-shaped to shortly tubular. Both *Mussaenda grandibracteata* and *M. scandens* have extremely short calyx tubes (1.5–2.5 mm) comparable to those of some African *Mussaenda* species (e.g., *M. tenuiflora* Benth., *M. isertiana* DC., and *M. debeauxii* Wernham). Longer calyx tubes reaching to 8 mm or more are present in *M. multibracteata* and some African *Mussaenda* (e.g., *M. elegans*). The shape and size of calyx lobes vary and are taxonomically valuable for species identification in *Mussaenda*. In the Philippine species, calyx lobes are usually linear-lanceolate to subulate, or foliaceous (*M. multibracteata*), or greatly reduced to toothlike structures 1 mm long (*M. philippica* var. *philippica*), similar to those of some African (e.g., *M. polita* Hiern) and Asian species (e.g., *M. reinwardtiana* Miq.). The length of the calyx lobes in the Philippine *Mussaenda* may be categorized into: (a) 5 mm or less, (b) 6–10 mm, (c) 11–19 mm, and (d) 20 mm or more. Categories (a) and (b) are the most common, followed by (c) in six species (*M. acuminatissima*, *M. anisophylla*, *M. benguetensis*, *M. nervosa*, *M. palawanensis*, and *M. philippinensis*), and rarely (d) (*M. multibracteata*). In *M. benguetensis*, calyx lobes may be unequal, so that the same flower may have short and long lobes. Calyx lobes may also vary in the presence or absence of trichomes. Calyx lobes of Philippine *Mussaenda* are covered with trichomes on both sides, or only abaxially, or just along the middle part abaxially (*M. nervosa*). A rare condition of strongly reflexed calyx lobes was observed in *M. viridiflora*, quite comparable to the African *M. arcuata*.

CALYCOPHYLLS

What makes *Mussaenda* and other *Mussaendeae* (*Landiopsis*, *Pseudomussaenda*, and *Schizomussaen-*

←
Short, straplike, verrucose trichomes in long-styled flower morphs. —G. *Mussaenda liedae* Alejandro. Globular trichomes sparsely distributed in long-styled flower morphs. —H. *Mussaenda benguetensis* Elmer. Alternating short, straplike, and globular trichomes in long-styled flower morphs. A, taken from Alejandro 108 (UBT); B, from Pelzer 13555 (PNH); C, from the holotype of *M. liedae*, Alejandro 89 (UBT); D, from Alejandro 30 (PNH); E, from Alejandro 20 (UBT); F and G, from Alejandro 108 (UBT); H, from the paratype of *M. liedae*, Alejandro 88 (L).

da) attractive is the presence of enlarged, showy calyx lobes that are here referred to as calycophylls (Delprete, 1996). Previous studies (e.g., Bremekamp, 1937; Jayaweera, 1964) have used the presence and/or absence of calycophylls as the basis to delimit *Mussaenda*. However, a recent molecular phylogenetic study showed that various African and Asian *Mussaenda* species both with and without calycophylls form a monophyletic group (Alejandro et al., 2005). All Philippine *Mussaenda* species possess the showy calycophylls, a good guide for locating them in the field at a distance. There are at least a few African *Mussaenda* species (e.g., *M. arcuata* and *M. elegans*), Asian *Mussaenda* (e.g., *M. uniflora*), and three Mussaendeae (*Bremeria*, *Heinsia*, and *Neomussaenda*) that do not bear calycophylls.

Calycophylls, composed of an expanded sepaloïd blade and stalk, are occasionally produced by a certain terminal flower of a cyme and correspond generally to only one of the five calyx lobes of a single flower, except in *Mussaenda philippica* var. *aurorae*, in which all five calyx lobes develop into calycophylls. The shape of calycophylls is usually ovate to elliptic, or rarely orbicular (*M. liedae*). The blades vary from 3–13 × 2–8.5 cm, usually with five longitudinal nerves, typically white or yellowish white (*M. grandifolia*, *M. milleri*, *M. pinatubensis*, and *M. scandens*). There are some reported African *Mussaenda* with vivid, striking colors like yellow-orange or carmine-red (*M. erythrophylla*).

COROLLA

Corolla tubes in *Mussaenda* are usually cylindrical or infundibular, slender or curved, and much longer than the lobes. A swollen part at the insertion of the anthers is typically observed in *Mussaenda* species with cylindrical tubes. Length and indumentum of corolla tubes are good characters to separate species in *Mussaenda*. In the Philippine species, corolla tubes vary in length from 1 to 4 cm. In most species they are 2–3 cm long or between 3 and 4 cm (e.g., *M. albiflora* Merr., *M. attenuifolia*, and *M. ustii*), and rarely less than 2 cm (*M. lanata*). Longer corolla tubes are rarely found in some African *Mussaenda* with 4 cm or more (e.g., *M. isertiana*) and Asian *Mussaenda* with 6 cm (e.g., *M. pluvialis* S. Moore). In Mussaendeae, extremely large corolla tubes reaching 5–15 cm in length characterize *Bremeria*.

The outer part of the corolla tubes in *Mussaenda* is typically covered with trichomes that extend to the abaxial side of the corolla lobes, or with few scattered trichomes (e.g., *M. grandibracteata*); often the lower part of some species becomes nearly glabrous after anthesis, rarely completely glabrous (e.g., *M. co-*

rymbosa Roxb. and *M. scratchleyi* Wernham). The inner lower half of the corolla below the stamens is glabrous in *Mussaenda*, whereas in other Mussaendeae the whole inner part of the corolla is covered with trichomes (e.g., *Bremeria*). In its upper portion, the corolla tube is usually covered with unicellular, yellow trichomes (Fig. 1C–H), rarely glabrous as in *M. grandifolia*. Variation of trichomes inside the corolla, which was not documented in Jayaweera's (1964) revision or by any other author, is an important character in recognizing some Philippine *Mussaenda*. Generally, heterostylous *Mussaenda* possess distinct disparate flat trichomes inside the corolla. In short-styled flower morphs, the trichomes are dense, long, not striate, ribbon-like (Fig. 1C, D) and extending to the base of anthers. In contrast, the trichomes of long-styled flower morphs are sparse, short, striate, ribbon-like (Fig. 1E), or straplike (Fig. 1F), and/or verrucose, globular (Fig. 1G), and extend to the short filaments. In *M. benguetensis*, the trichomes of long-styled flower morphs are mixed or alternating short-strapped and globular (Fig. 1H). A combination of globular and ribbon-like trichomes near the base of anthers is a trend especially found in Palawan *Mussaenda* (*M. setosa* Merr. and *M. liedae*). The differentiation in type and density of trichomes between the two flower morphs is also observed in some African and Asian *Mussaenda* species. Robbrecht (1988) described a rare short longitudinal split in the base or middle of corolla tubes in some Rubiaceae genera including *Mussaenda*, reminiscent of *Stackhousia* Sm. (Celastraceae). However, this particular character was not observed in any Philippine *Mussaenda*.

The corolla lobes of Philippine *Mussaenda* are usually elliptic to ovate, rarely somewhat truncate (*M. lanata*), or linear-lanceolate (*M. albiflora*). Their sizes usually range from 1.2–10 × 1–6 mm, or rarely to 22 mm long (*M. albiflora*). The color is usually orange to yellow, or rarely white (*M. albiflora*), or a combination of yellow median ridges and white margins (*M. ustii*). A more spectacular coloration is present in African *Mussaenda* (e.g., *M. elegans*) that have pink to orange or bright red corolla lobes.

Bridson and Verdcourt (1988) distinguished *Pseudomussaenda* from *Mussaenda* by having apical filiform appendages at the tip of each corolla lobe. However, Puff et al. (1993) correctly argued that these appendages also occur within *Mussaenda*, where half of the Philippine species bear them. Therefore, the presence or absence of such appendages is not reliable for generic delimitation in Mussaendeae.

Jayaweera (1964) used the occurrence of trichomes surrounding the corolla opening to delimit Asian *Mussaenda*. He emphasized that such trichomes are absent in the Philippine taxa but present in the species of India and Sri Lanka. Based on our recent collections, some Philippine *Mussaenda* are observed with trichomes in the corolla opening (e.g., *M. benguetensis*, *M. magallanensis* Elmer, and *M. ustii*).

AESTIVATION

There are two main types of corolla aestivation in the Mussaendeae, imbricate and valvate (see Robbrecht, 1988: fig 29). Imbricate aestivation is found in both *Heinsia* and *Landiopsis*. Valvate aestivation occurs in three variations: induplicate-valvate (*Neomussaenda*, *Pseudomussaenda*, and *Schizomussaenda*), reduplicate-valvate (*Mussaenda*), and a combination of induplicate- and reduplicate-valvate (*Bremeria*). The last two valvate aestivation types are reliable characters to delimit both *Mussaenda* and *Bremeria* (Alejandro et al., 2005).

ANDROECIUM

The stamens of Mussaendeae are separate, of equal sizes, and inserted around the middle of the corolla tube. In *Mussaenda*, the stamens of short-styled flower morphs are typically inserted above the middle of the corolla, rarely at the middle (e.g., *M. isertiana*). In contrast, the stamens of long-styled flower morphs are located at the middle, and rarely below the middle of the corolla (e.g., *M. setosa* and *M. afzeliioides* Wernham).

The anthers of Philippine *Mussaenda* are usually linear, dorsibasifixed, dehiscing along longitudinal slits, and typically bilobed at the base. The short-styled flower morphs usually have longer anthers than the long-styled flower morphs. Generally, the filaments of anthers are short, filiform, usually adhering to the corolla tubes almost along their entire length, and glabrous except for a few trichomes found in *M. benguetensis*.

GYNOECIUM

The cylindrical-turbinate ovary of *Mussaenda* is usually bicarpellate, or rarely 3- or 4-locular (e.g., *M. nannanii* Wernham). All Philippine species are bicarpellate; the locules are pluriovulate and separated by a septum. Puff et al. (1993: figs. 3–8) demonstrated the anatomical details of the ovary and fruits among African *Mussaenda*, *Pseudomussaenda*, and *Schizomussaenda*. Similar features of the ovary and fruits were observed in Philippine *Mussaenda*. The placenta is peltate, inserted to most of the length

of the septum, and T-shaped in cross-section with the ends of the cross-bar incurved. The ovules are numerous and embedded in a soft pulp.

The styles of *Mussaenda* are usually slender and glabrous. In the Mussaendeae, only *Bremeria* is characterized by pubescent styles as one of its synapomorphies. The length of styles in the Philippine *Mussaenda* ranges from 1 to 8 mm in short-styled flowers and from 10 to 25 mm in long-styled flower morphs, except for long-styled flowers in *M. lanata*, which are 5–7 mm. A well-developed, fleshy, annular, glabrous disk that is persistent in the fruit surrounds the base of the style. The stigma of *Mussaenda* is elongated and bilobed, and ranges from 1 to 4 mm in short-styled and from 3 to 12 mm in long-styled flower morphs. The short stigmatic lobes are usually spreading, while the longer lobes are recurving. The two stigmatic arms are semi-exserted in a few Philippine species of long-styled flower morphs (e.g., *M. magallanensis*, *M. ustii*, and *M. liedae*).

FRUITS

Previous studies used fruit types (berry vs. capsular) as one of the main bases for delimiting *Mussaenda*. Segregates *Pseudomussaenda* and *Schizomussaenda* are characterized by dehiscent, capsular fruits, whereas *Mussaenda* has indehiscent, berry-like fruits. In other Mussaendeae, the fruits of *Landiopsis* are dehiscent capsules; those of both *Heinsia* and *Bremeria* are fleshy and indehiscent; and only *Neomussaenda* is distinguished by its drupaceous fruits.

The fruits of *Mussaenda* are pedicellate, generally warty, ellipsoid to obovoid, or rarely globose, green when young, and brown to blackish at maturity, as far as observed. *Mussaenda* fruits rarely exceed 2 cm in length. The average size in the Philippines ranges from 1–2 × 0.6–1.4 cm. Vertical ridges are usually absent, rarely prominent (e.g., *M. acuminatissima* and *M. albiflora*). Conspicuous annular disks typically crown the fruits, and persistent calyces were observed in five Philippine species (*M. acuminatissima*, *M. anisophylla*, *M. multibracteata*, *M. philippinensis*, and *M. vidalii*). In some species, the calyx lobes may reach a length of 1 cm and then often get damaged in the fruit stage. The exocarp is usually covered with trichomes, rarely glabrous (e.g., *M. nervosa* and *M. scandens*). The mesocarp ranges from 0.3 to 1.2 mm in thickness.

SEEDS AND EXOTESTA

The seeds of *Mussaenda* are usually small, numerous, more or less angular to rounded, laterally

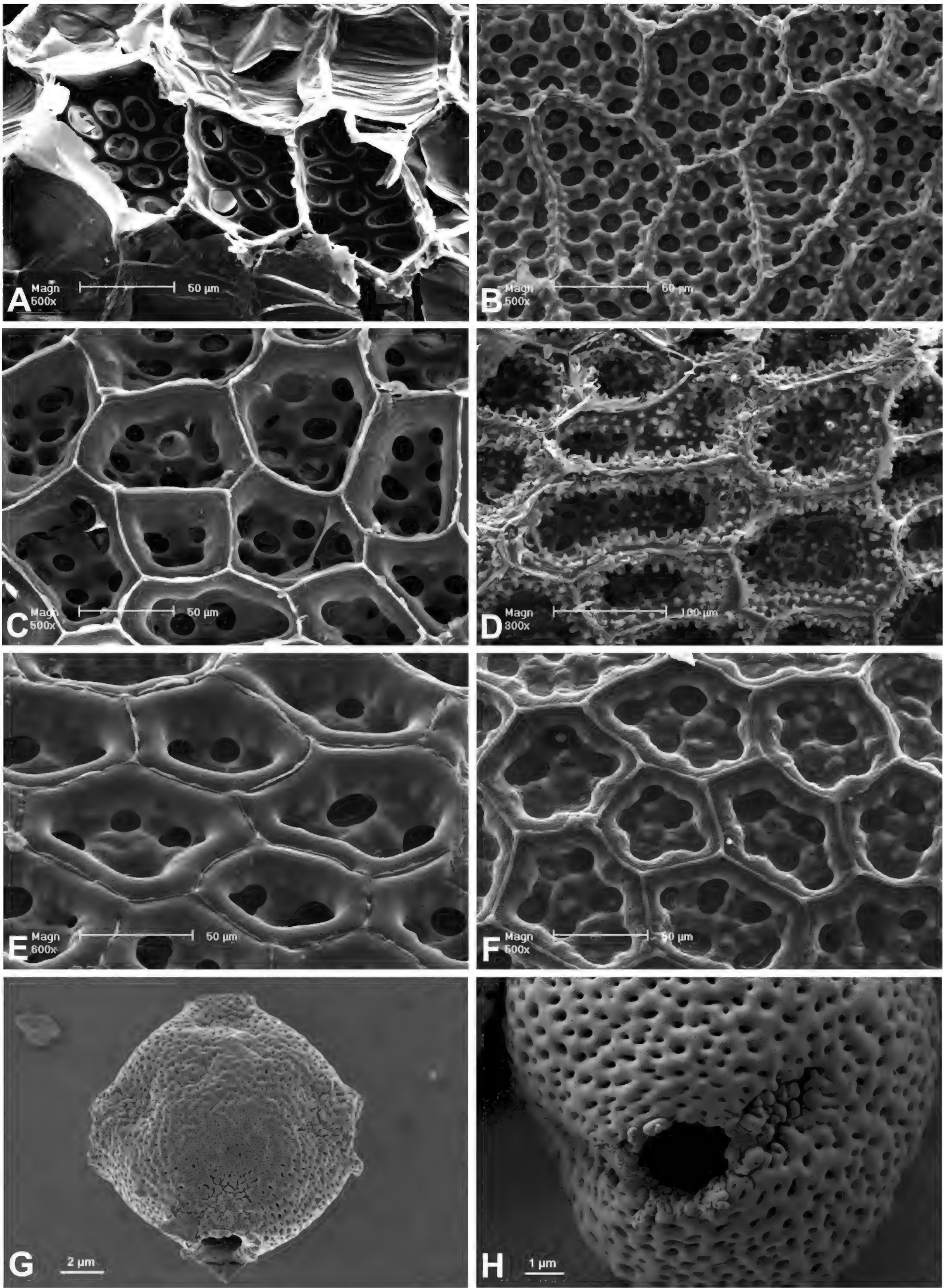


Figure 2. A–F. Seed exotesta cells of Mussaendeae, the outer tangential walls removed in B–F, but retained in A. —A. *Mussaenda debeauxii* Wernham from Africa. —B. *Pseudomussaenda flava* Verdc. from Africa. —C. *Bremeria pervillei* (Wernham) Razafim. & Alejandro from Madagascar. —D. *Heinsia crinita* (Afzel.) G. Taylor from South Africa. —E. *Mussaenda acuminatissima* Merr. —F. *Mussaenda magallanensis* Elmer. G, H. Pollen of *M. anisophylla* S. Vidal. —G. Four-colporate pollen. —H. Foveolate tectum. A, taken from Schoenmaker 388 (WAG); B, from Friis *et al.* 8030 (BR); C, from Humbert 18745 (P); D, from Sonké 308 (BR); E, taken from the lectotype of *M. acuminatissima*, Ramos Bureau of Sci. no. 33133 (NY); F, from Alejandro 3 (UBT); G and H, from Alejandro 65 (Univ. Santo Tomas Hb.).

flattened, and brown to black. The size of seeds is less than 1 mm in all Philippine species, although seeds of some African *Mussaenda* can exceed 1 mm (e.g., *M. arcuata*). Variation in size and shape of seeds often occurs in a single fruit. The seed coat is exotestal, a typical character in Rubiaceae.

In the Mussaendeae, the exotesta cells are polygonal in surface view (described as reticulations by Jayaweera, 1963, 1964). The outer tangential walls of exotesta are thin and more or less smooth (Fig. 2A), while the radial walls are considerably thickened (Fig. 2A–F). Prominent large pits are present on the inner tangential walls (Fig. 2A–F) except for *Schizomussaenda* with small pits (Puff et al., 1993: fig. 11). In Philippine *Mussaenda*, these perforations vary in number from two to 10; only few reach more than 10 (e.g., *M. chlorantha* and *M. nervosa*). There are African *Mussaenda* characterized by up to 14 perforations (e.g., *M. debeauxii*: Fig. 2A), or up to 20 (e.g., *M. soyauxii* Büttner). *Pseudomussaenda* has even 20 or more perforations (*P. flava* Verdc.: fig. 2B). Seed perforations of both *Bremeria pervillei* (Wernham) Razafim. & Alejandro (Fig. 2C) and *Heinsia crinita* (Afzel.) G. Taylor (Fig. 2D) are within the range of *Mussaenda*. The number of perforations sometimes varies, even in the inner tangential walls of a seed.

Seed ornamentation may be present or absent in Mussaendeae. Tubercular thickenings along the radial and inner tangential walls can be numerous, well-protruding (*Heinsia crinita*: Fig. 2D), or fewer and less conspicuous (*Pseudomussaenda flava*: Fig. 2B), or slightly prominent (e.g., *Mussaenda acuminatissima*: Fig. 2E; *M. magallanensis*: Fig. 2F; and *M. ustii*), or absent (e.g., *M. debeauxii*: Fig. 2A; and *M. tristigmatica* Cumm.).

POLLEN, HETEROSTYLY, AND DIOECY

Pollen studies are available for Mussaendeae, particularly African and Asian *Mussaenda* (Gideon, 1989; Puff et al., 1993; Andersson, 1996). In Philippine *Mussaenda*, pollen grains are usually tetracolporate (Fig. 2G), but occasionally tricolporate grains were observed (cf. Puff et al., 1993). The average diameter ranges from 10.8 μm in *M. liedae* to 19.8 μm in *M. benguetensis* (Alejandro, pers. obs.). Pollen exine is typically foveolate (Fig. 2H), as previously described by Andersson (1996) for Afro-Asian *Mussaenda* and *Pseudomussaenda*.

It is worth noting that long-styled morphs of the flower typically lack (fertile) pollen and that all pollen measurements were taken from short-styled flower morphs. Jayaweera (1964) previously observed that the long-styled flower morphs do not shed or form

pollen, but he failed to mention the dioecism of the genus. All populations of the Philippine *Mussaenda* comprise two style-length morphs. The short-styled flower morphs represent the staminate condition in which the gynoecium ceases to grow and remains sterile, while the long-styled flower morphs are pistillate and have sterile anthers. This condition was earlier observed in *M. pubescens* W. T. Aiton and termed as cryptic dioecy (Li et al., 2010).

CHROMOSOMES

Chromosome numbers of over 30 taxa of African and Asian *Mussaenda* have been counted, and invariably $x = 11$ has been the basic chromosome number (Priyadarshan & Ramachandran, 1984; Kiehn, 1986, 1995, 1996; Philip & Mathew, 1988; Puangsomlee & Puff, 2001). These studies unanimously report that *Mussaenda* species are diploid, and polyploidy seems to be relatively insignificant. Chromosome counts from Philippine plant material are available for *M. philippica* s. str. and *M. philippica* var. *aurorae*, and the three cultivars Doña Aurora, Doña Luz, and Sirikit. These all possess $2n = 22$ (Priyadarshan & Ramachandran, 1984; Philip & Mathew, 1988). We also investigated root tips of *M. philippica* var. *philippica* (Alejandro 10164) propagated at the University of Bayreuth following Tjio and Levan (1950) and Snow (1963). We counted $2n = 22$ chromosomes from somatic metaphases. The chromosomes are fairly uniform in size, measuring about 1.15 μm in length. The basic chromosome number of $x = 11$ is the most widespread in flowering plants, also consistent in Ixoroideae (De Block, 1998) and several woody tribes of Rubiaceae such as the Gardenieae, Psychotrieae p.p., Anthospermeae, and Pavetteae (Philip & Mathew, 1988; Robbrecht, 1988; Corrêa et al., 2010).

POLLINATION AND DISPERSAL

The conspicuous, brightly colored calycophylls contrast with the large, dark green leaves of *Mussaenda* plants, or surrounding vegetation, and serve as a visual signal for attraction of flower visitors and pollinators. Borges et al. (2003) demonstrated that the white calycophylls of *M. frondosa* L. absorb ultraviolet light, whereas reflectance for longer wave lengths is much higher than that of the leaves. Predominantly, butterfly pollinators are attracted. For *M. pubescens* in Hong Kong, Corlett (2001) observed butterfly species of *Papilio* L. and *Graphium* Scopoli (Papilionidae) as frequent visitors and apparent pollinators of the flowers. The high reflectance of the calycophylls possibly also causes an effective attraction of nocturnal lepidopteran pollinators such as the

Sphingidae (*Cephonodes hylas* L., species of *Macroglossum* Scopoli), as has been demonstrated by Naiki and Kato (1999) for *M. parviflora* Miq. Removal of calycophylls in *M. frondosa* significantly decreases pollinator attraction (cf. Borges et al., 2003), while nectar-robbing bees continue to find the flowers. For the Philippine *Mussaenda*, any pollination data are still missing. Birds have been observed in the field to eat the ripe fruits of *Mussaenda* (Alejandro, pers. obs.) and may be important disseminators of the seeds.

HABITAT AND DISTRIBUTION

Mussaenda thrive in diverse climatic and environmental conditions and in a wide range of soil types. Recent collections in the Philippines were made between 0 and 3000 m, and from habitats ranging from coastal scrubs and thickets, disturbed roadsides, ravines, along river and stream banks, secondary and primary forests, savanna forests, and lowland or montane forests. *Mussaenda* species occasionally grow in ultramafic soils; they seem to prefer more well-drained, clayey, loamy, or sandy, humid soils. Few species prefer the canopy of the thick forest, but the majority flourish in the semi-shade or open forest, displaying their attractive calycophylls and sometimes extending their branches over the neighboring shrubs. The wild *Mussaendas* are similar to the propagated varieties, requiring full sunlight for healthier and more colorful blooms. *Mussaenda* grown under semi-shade or filtered light are lanky with fewer and less colorful calycophylls (Rosario, 1998). Several African and Asian species (e.g., *M. erythrophylla*, *M. parvifolia* Valetton, and *M. philippica* var. *philippica*) are grown as ornamentals both in and outside their natural distribution ranges and may be found in the Philippines.

Mussaenda is widely distributed throughout tropical Africa eastward to eastern and southeastern Asia, to southernmost Japan, and southward to New Guinea and Australia. In the Philippines, most *Mussaenda* species occur in Luzon (extending to the Batanes Islands), followed by the endemic species from Mindanao (*M. attenuifolia*, *M. nervosa*, *M. scandens*, and *M. vidalii*), Palawan (*M. grandifolia*, *M. liedae*, *M. palawanensis*, and *M. setosa*), and the Visayas (*M. albiflora*, *M. ustii*, and *M. viridiflora*). *Mussaenda philippica* var. *philippica* is the only taxon distributed almost throughout the Philippines, extending eastward to the Caroline group and southward to the Solomon and Fiji Islands.

ECONOMIC USES

Aside from its ornamental purposes, indigenous use of *Mussaenda* is not common in the Philippines

based on personal interview, literature, and herbarium label information. Only a few *Mussaenda* species are used medicinally such as *M. anisophylla* (asthma), *M. vidalii* (antiseptic or ophthalmic drops), *M. philippica* var. *philippica* (stomach and headache, snake bites, dysentery, minor chest pains, jaundice, and emollient) (Guerrero, 1921). Salvoza (1948) included *M. philippica* var. *philippica* in the list of Philippine trees and shrubs yielding crude drugs. Some Philippine *Mussaenda* have various local uses such as for fuel, handicrafts, small furniture, and even for agricultural rituals (Alejandro, pers. obs.).

TAXONOMIC TREATMENT OF PHILIPPINE *MUSSAENDA*

Mussaenda Burm. ex L., Sp. Pl. 1: 177. 1753. TYPE: *Mussaenda frondosa* L.

Asemanthia (Stapf) Ridl., Bull. Misc. Inform. Kew 1939(10): 599. 1940. TYPE: *Asemanthia coccinea* (Stapf) Ridl. [= *Mussaenda coccinea* Stapf, nom. illeg.]

Spallanzania DC., Prodr. [A. P. de Candolle] 4: 406. 1830 [late Sep. 1830]. TYPE: *Spallanzania corymbosa* DC.

Trees or shrubs, rarely scandent or suffrutices, to 8 m tall; young twigs somewhat flattened to terete, green to grayish green, or brown, glabrous or variously indumented, the trichomes cylindrical, white, or brown to reddish brown color; older branches (sub)terete, lenticellate, bark easily peeled, reddish to grayish brown, or brown, glabrous or with few scattered trichomes. Leaves opposite and decussate, sometimes anisophyllous, variously indumented, rarely glabrous; leaf blades ovate or elliptic, rarely obovate to orbicular, (sub)coriaceous to membranous; margins entire, rarely slightly sinuate, glabrous or ciliate, apex acute or acuminate to subcaudate, rarely conduplicate, base cuneate or attenuate to obtuse, secondary veins brochidodromous, in 5 to 15 (to 18) pairs, usually prominulous, rarely sunken above; petioles to 8 cm, rarely subsessile; stipules interpetiolar, usually triangular, or ovate, sometimes basally fused forming a ring around the node, persistent or deciduous, apices bifid 1/8 to 3/4 of their length, the lobes erect and rarely spreading away from each other, abaxially with indument, adaxially with indument all over or only at the base and/or apex, colleters few or numerous, in continuous rows and/or in groups of 2 at the stipule base. Inflorescences terminal, rarely becoming pseudoaxillary, cymose corymbs, ultimate elements regular, sympodial-dichasial branching, spreading or congested, glabrous or variously hairy; bracteate, bracts linear or lanceolate to ovate, entire or trilobed with the lateral lobes always shorter, adaxially variously indumented, abaxially glabrous to pubescent all over or rarely with tuft of trichomes only at the

base. Flowers heterostylous and/or dioecious, 5-merous, or rarely aberrantly 6-merous, congested (calycophyllous pseudanthia), odorless, rarely sweet-scented, shortly pedicellate; pedicels to 7 mm, pubescent, rarely glabrous; calyx tubes cup-shaped to shortly tubular, or extremely reduced, usually indumented, rarely glabrous; calyx lobes extremely short or long, linear to lanceolate or ovate, rarely foliaceous, rarely strongly recurved, abaxially with trichomes, adaxially glabrous or with trichomes, occasionally with a single calycophyll, rarely with 5 calycophylls; colleters usually in sinuses between calyx lobes, rarely in a row at the base; calycophylls restricted to the terminal flowers of inflorescence, elliptic to ovate, or orbicular, 5(to 7)-nerved, white, or cream to yellowish white, glabrous or pubescent along the nerves of both sides, calycophyll margins glabrous or ciliate, apex apiculate or acute to acuminate or subcaudate, base cuneate to attenuate or obtuse, calycophyll stalks 1–3.5 cm long, usually pubescent; corolla salverform to narrowly funnelform, variously indumented, corolla tube cylindrical or infundibular, sometimes curving, usually forming a distinctly swollen part around anthers when cylindrical, yellowish green/white or greenish white/yellow to white, with or without trichome tuft surrounding the opening, typically with unicellular trichomes inside; short-styled flower morphs with dense long, flat, unstriated, ribbon-like trichomes extending to the base of anthers from the top of corolla; long-styled flower morphs with sparse short, flat, striated, ribbon-like or straplike, and/or rarely with verrucose, globular trichomes extending to the short filaments from the top of corolla; lobes valvate-reduplicate, elliptic to ovate,

rarely linear to lanceolate, or somewhat truncate to orbicular, median ridge distinct, corresponding to the infolded part of the lobe before anthesis, orange to yellow, rarely white, abaxially pubescent, adaxially papillate; apex with or without filiform appendages, rarely recurved; stamens 5, included, glabrous, usually inserted in distal quarter, or immediately below the opening in short-styled flowers, around the middle in long-styled flower morphs, filaments short, fused for most of their length with the corolla tube; anthers linear, dorsibasifixed, bilobed at the base, dehiscing by longitudinal slits, the apex acute or obtuse; pollen colporate, 10.35–19.80 μm diam., exine foveolate, apertures 4, rarely 3; ovary cylindric to turbinate, bilocular; annular disk conspicuous, glabrous in both short- and long-styled flower morphs; style cylindrical, glabrous; stigma lobes 2, smooth or papillose, included or semi-exserted, usually recurved in long-styled flower morphs; carpellary placenta peltate, T-shaped with the ends incurved in cross-section; ovules numerous, embedded in fleshy placentas. Fruits fleshy, berry-like, ellipsoid to obovoid or globose, warts usually present, vertical ridges rarely prominent, brownish black when ripe, calyces deciduous or persistent, glabrous or pubescent; exocarp thin; mesocarp well-developed; seeds \pm angular, less than 1 mm; exotesta cells polygonal, outer tangential walls thin and \pm smooth, radial tangential walls thickened, inner tangential walls porous, tuberculate thickenings rarely prominent. Chromosome number: $2n = 22$ (Priyadarshan & Ramachandran, 1984; Kiehn, 1986, 1995, 1996; Philip & Mathew, 1988; Puangsomlee & Puff, 2001).

KEY TO THE PHILIPPINE SPECIES OF *MUSSAENDA*

- 1a. Stipules distinctly diverging, broadly oblong to broadly ovate; corolla tube with mixed or alternating globular and straplike trichomes inside long-styled flower morph 5. *M. benguetensis* Elmer
- 1b. Stipules at the most slightly diverging, triangular to ovate; corolla tube with either globular, or strap- or ribbon-like trichomes inside long-styled flower morph.
 - 2a. Leaf blades with distinctly sunken midrib and veins adaxially; calyx lobes with trichomes only along the median portion externally 15. *M. nervosa* Elmer
 - 2b. Leaf blades with prominulous midrib and veins adaxially; calyx lobes with trichomes all over surface externally 3.
 - 3a. Calyx tube 6–8 mm long; calyx lobes foliaceous, $20\text{--}27 \times 6\text{--}7$ mm 14. *M. multibracteata* Merr.
 - 3b. Calyx tube 1.5–6 mm long; calyx lobes not foliaceous, less than 20×3 mm 4.
 - 4a. Young twigs and inflorescences glabrous or puberulous.
 - 5a. Stipules bifurcate for 1/8 of their length; bracts numerous, 2.5–5 mm wide 7. *M. grandibracteata* Alejandro
 - 5b. Stipules bifurcate for 1/4 to 3/4 of their length; bracts few, 0.8–1.7 mm wide 6.
 - 6a. Leaf apices strongly conduplicate; calyx tube 1.8–2.5 mm long; corolla without filiform apical appendages 20. *M. scandens* Elmer
 - 6b. Leaf apices not conduplicate; calyx tube 3–7 mm long; corolla with filiform apical appendages 7.
 - 7a. Calyx lobes $7\text{--}8 \times 0.8\text{--}1$ mm; calycophylls yellowish white 19. *M. pinatubensis* Elmer
 - 7b. Calyx lobes $1.5\text{--}3.5(\text{--}7) \times 1.5\text{--}2$ mm; calycophylls white or cream 17. *M. philippica* A. Rich.

- 4b. Young twigs and inflorescences prominently indumented 8.
- 8a. Corolla tube infundibular, bulging very weakly or slightly around anthers.
 - 9a. Leaf blades ovate or obovate to orbicular, not elliptic; corolla tube 1.1–1.5 cm long 9. *M. lanata* C. B. Rob.
 - 9b. Leaf blades ovate or elliptic to obovate; corolla tube 2–4 cm long 10.
 - 10a. Young twigs and inflorescences densely velvety; corolla tube glabrous internally in long-styled flower morph 8. *M. grandifolia* Elmer
 - 10b. Young twigs and inflorescences hirsute or pilose; corolla tube always with trichomes internally in long-styled flower morph 11.
 - 11a. Calyx lobes linear to narrowly lanceolate; fruit calyces persistent 12.
 - 12a. Stipules with sparse indument only at adaxial base; fruits sparsely warty, with prominent vertical ridges 1. *M. acuminatissima* Merr.
 - 12b. Stipules with sparse indument evenly distributed on adaxial side; fruits smooth, without vertical ridges 18. *M. philippinensis* Merr.
 - 11b. Calyx lobes lanceolate or subulate to ovate; fruit calyces deciduous or subpersistent 13.
 - 13a. Corolla lobes 5–10 × 3–3.5 mm, with filiform apical appendages 16. *M. palawanensis* Merr.
 - 13b. Corolla lobes 4–5 × 4–6 mm, without filiform apical appendages 14.
 - 14a. Trees, with pilose indumentum; stipules adaxially densely pilose; fruits obovoid, 1–1.4 cm long 6. *M. chlorantha* Merr.
 - 14b. Erect or scandent shrubs, with hirsute indumentum; stipules adaxially sparsely hirsute only at the apex and base; fruits ellipsoid, 1.5–2.2 cm long 23. *M. vidalii* Elmer
- 8b. Corolla tubes cylindrical, bulging distinctly around anthers 15.
- 15a. Corolla lobes purely white or the bases and median ridges green-tinged 16.
- 16a. Leaf blades densely hirsute abaxially; flowers odorless; calyx lobes not recurved, 6–8 mm long; corolla lobes linear-lanceolate, usually 9–12 mm long, sometimes to 22 mm 2. *M. albiflora* Merr.
- 16b. Leaf blades sparsely pubescent abaxially; flowers sweet-scented; calyx lobes strongly recurved, 3–4 mm long; corolla lobes ovate, 8–10 mm long 24. *M. viridiflora* Alejandro
- 15b. Corolla lobes orange to yellow with white margins 17.
- 17a. Inflorescences with numerous bracts 18.
- 18a. Stipules adaxially densely indumented throughout; corolla densely hirsute in bud stage; corolla lobes 5–6 mm long, orange to yellow 3. *M. anisophylla* S. Vidal
- 18b. Stipules adaxially sparsely indumented only at base; corolla pilose in bud stage; corolla lobes 7–13 mm long, yellow with white margins 22. *M. ustii* Alejandro
- 17b. Inflorescences with few bracts 19.
- 19a. Stipules with adaxial indument only at base; calyx lobes with trichomes only abaxially; corolla tube with short, globular trichomes inside long-styled flower morphs 20.
- 20a. Leaf blades setose abaxially; calyx tubes 3–3.5 mm long; calyx lobes 4–6 mm long; corolla buds densely hirsute 21. *M. setosa* Merr.
- 20b. Leaf blades sparsely hirsute abaxially; calyx tubes 5–6 mm long; calyx lobes 2–4 mm long; corolla buds densely pubescent 10. *M. liedae* Alejandro
- 19b. Stipules with adaxial indument all over surface; calyx lobes with trichomes on both surfaces; corolla tube with short, flat, straplike trichomes inside long-styled flower morphs 21.
- 21a. Young twigs and inflorescences densely pubescent; leaf bases attenuate 4. *M. attenuifolia* Elmer
- 21b. Young twigs and inflorescences mainly hirsute; leaf bases cuneate or obtuse 22.
- 22a. Young twigs and inflorescences with reddish brown trichomes; calycophylls yellowish white, with base attenuate 13. *M. milleri* Elmer ex Alejandro
- 22b. Young twigs and inflorescences with white to gray or brown trichomes; calycophylls white, with base cuneate.
- 23a. Leaf margins glabrous; flower pedicels 0.5–1.5 mm long; calyx lobes 3.2–14 × 1.2–4 mm 11. *M. macrophylla* Wall.
- 23b. Leaf margins ciliate; flower pedicels 2–2.5 mm long; calyx lobes 4–5 × 0.5–1 mm 12. *M. magallanensis* Elmer

1. *Mussaenda acuminatissima* Merr., Philipp. J. Sci. 17(Pt. C): 436–437. 1920. TYPE: Philippines. Ilocos Norte: Luzon, Mt. Nagapatan, 18°16'N, 120°37'E, 8 Aug. 1918, *Bureau of Science* 33133 [*M.*] *Ramos* (lectotype, designated by Jayaweera [1964: 105], NY [barcode] 00132303!). Figure 3.

Shrubs 3–3.5 m tall; young twigs green, hirsute, the trichomes more than 12-celled, brown; older branches lenticellate, reddish brown, glabrous. Leaf blades ovate or elliptic, 9–16 × 4.5–8.5 cm, membranaceous to (sub)coriaceous, sparsely pubescent on both sides, especially on the midrib and veins underneath, margins ciliate, apex acuminate to subcaudate, flat, base long attenuate; secondary veins in 10 to 12 pairs, prominent above; petioles 1.3–2.5 cm, densely pubescent; stipules triangular, 7–15 × 2–3 mm at the base, deciduous, abaxially with dense indument, adaxially with sparse indument only at the base of stipule, bifid for 1/4 to ± half of length, the lobes not diverging; colleters numerous, in groups of 2 at stipule base. Inflorescences terminal, sometimes axillary from terminal leaf pairs, congested, densely hirsute; bracts few, linear to narrowly lanceolate, entire or bilobed, 5–9 × 1–2.5 mm, sparsely pubescent underneath, glabrous or sparsely pubescent above; flower pedicels 2–2.5 mm, densely strigose. Flowers odorless, with only long-styled flower morphs seen; calyx tubes cup-shaped to shortly tubular, 3.5–4 mm, densely hirsute; calyx lobes linear to narrowly lanceolate, erect, 8–15 × 1–1.4 mm, hirsute on both sides, occasionally with a single calycophyll; colleters as 1 pair per lobe, in sinuses between calyx lobes; calycophylls with blades elliptic or elliptic to ovate, 5-veined, 4–11.2 × 5.5–6 cm, white or cream, sparsely pubescent especially along nerves on both surfaces, margins ciliate, apex acuminate, base cuneate, calycophyll stalks 1.5–2.2 cm, densely pubescent; corolla in buds densely hirsute, becoming hirsute only in upper half and with few scattered trichomes below in open flowers; corolla tubes infundibular, swollen portion around anthers indistinct, 2.3–2.5 cm long, cream, with tuft of trichomes surrounding the opening internally; in long-styled flower morphs with sparse short, striate, ribbon-like trichomes internally to the short filaments from the top; corolla lobes ovate, 3.5–4.5 × 3.5–4 mm, yellow or yellow-orange, abaxially hirsute, adaxially papillate, at apex spreading, without filiform apical appendages; stamens inserted around middle of the corolla tube in long-styled flower morphs, filaments glabrous, anthers linear, 4–4.5 mm in long-styled flower morphs, glabrous, apex acute; pollen diameter to 14.85 µm, apertures 4; ovary 3–3.5 × 2–2.5 mm, style 10–15 mm in long-styled flower morphs, stigma 5–7 mm, smooth, erect, included in long-styled flower morphs.

Fruits ellipsoid to obovoid, 1–1.5 × 0.8–1 cm, with sparse warts, vertical ridges 8 to 10; calyces persistent, sparsely to densely hirsute; mesocarp 0.4–0.6 mm thick; fruiting pedicels 3–4 mm, densely hirsute; seeds 0.46–0.6 × 0.43–0.56 mm; exotesta cells with 3 to 5 pores on inner tangential walls, tuberculate thickenings absent.

Local names. Katuday-bantay (Ilk); Tinga-tinga (Tag), according to Alejandro (pers. obs.).

Phenology. *Mussaenda acuminatissima* has been observed to flower from August to October, and fruit in August, and November to December.

Distribution and habitat. *Mussaenda acuminatissima* appears to be locally rare and restricted to the provinces of Ilocos Norte and Batangas of Luzon. The species has been collected in primary and secondary forest edges, on ultramafic soils, from sites at elevations from 250 to 700 m.s.m.

Discussion. Merrill (1920: 437) mentioned only the one collection, “*Bur. Sci.* 33133 *Ramos*,” in the protologue for *Mussaenda acuminatissima*. This was later considered as “type” and specified to the herbarium of deposit as “NY–lectotype” by Jayaweera (1964: 104 and 105, respectively). As a Bureau of Science collection for the Flora of the Philippines, Merrill’s principal duplicate would have been deposited at PNH and was destroyed during World War II. The surviving duplicate at NY cited by Jayaweera as type was required after 1958 (Art. 40.1, McNeill et al., 2012) and specified the herbarium of deposit, *sensu* Articles 9.11 and 9.12.

This species is distinct from other hirsute Philippine *Mussaenda* with its short petioles only to 2.5 cm, narrow stipules with trichomes only at the base adaxially, few colleters on the calyx lobes, and warty fruits with prominent vertical ridges. So far the only recorded *Mussaenda* species in Ilocos Norte is *M. philippica* var. *philippica* and in Batangas, *M. anisophylla*. *Mussaenda acuminatissima* closely resembles *M. philippinensis* in the shape and size of the linear to narrowly lanceolate calyx lobes to 15 mm, which are persistent on the fruits, but the two species differ in the density of trichomes and in the shape of the leaves. In *M. acuminatissima*, the calyx lobes are hirsute but less pubescent to internally glabrate in *M. philippinensis*. Leaf blades are ovate to elliptic in *M. acuminatissima*, to 16 cm long, but are only elliptic in *M. philippinensis* but to 25-cm lengths.

Additional specimen examined. PHILIPPINES. **Luzon:** Batangas, Lobo, Mt. Mabilog, 13°38'N, 121°13'E, Alejandro 60 (L, PNH, UBT, *University of Santo Tomas Herbarium* [Univ. Santo Tomas Hb], US).

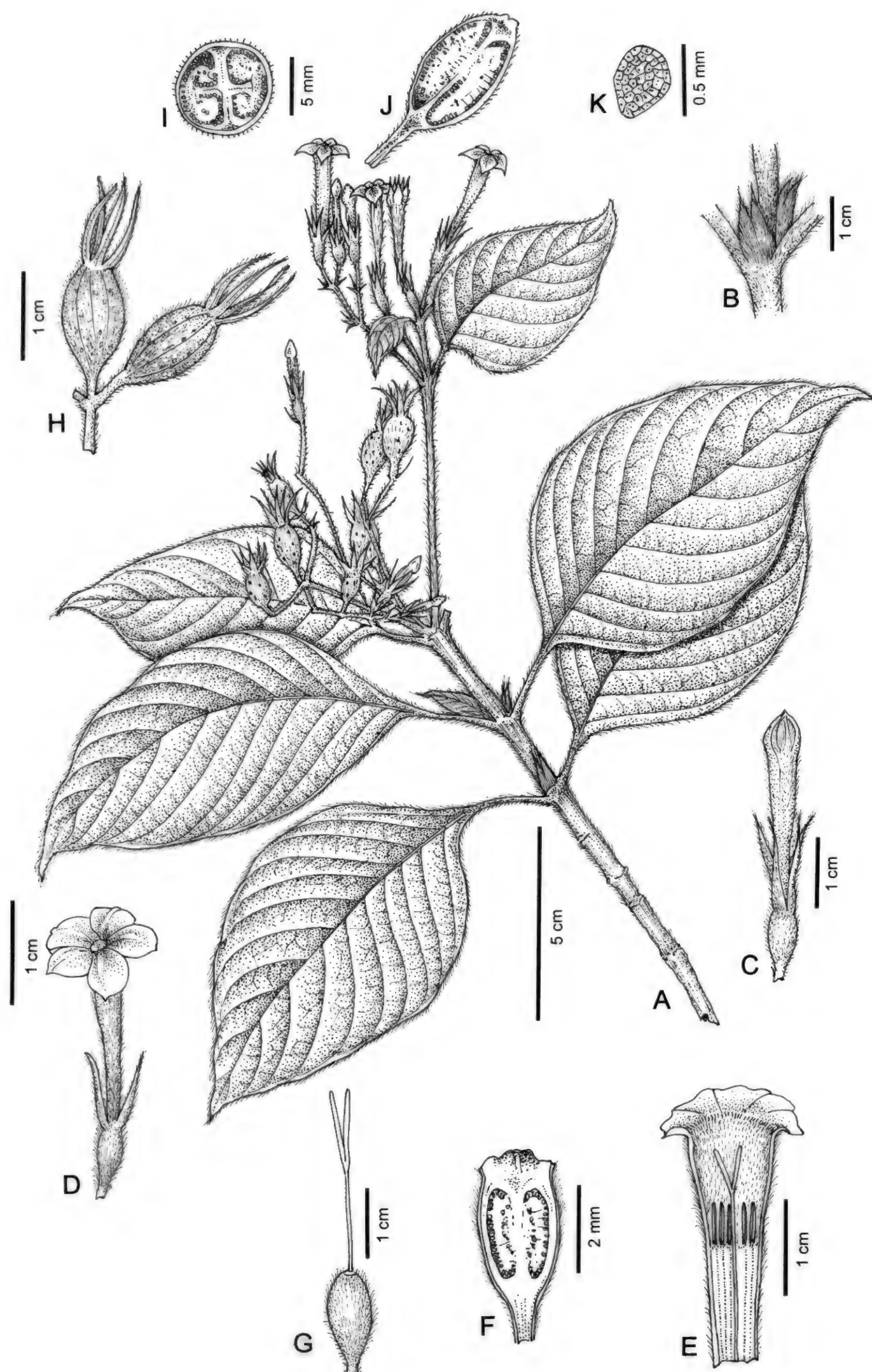


Figure 3. *Mussaenda acuminatissima* Merr. —A. Fertile branch with flowers and fruits. —B. Portion of stem with stipules. —C. Flower bud. —D. Open anthesal flower. —E. Long-styled flower morph, corolla tube dissected open in longitudinal section. —F. Longitudinal section through ovary. —G. Calyx, style, and stigma of long-styled flower morph, with the corolla and calyx lobes removed. —H. Fruits with vertical ridges and persistent calyces. —I, J. Fruit sections showing seed attachments to placentas, in cross and longitudinal sections, respectively. —K. Seed. A–D, H–K are taken from the lectotype *Ramos Bureau of Sci. no. 33133* (NY); E–G, from *Alejandro 60* (Univ. Santo Tomas Hb.).

2. *Mussaenda albiflora* Merr., Philipp. J. Sci. 5(Pt. C): 241–242. 1910. TYPE: Philippines. Negros Occidental, Sep. 1909, *Forest Bureau 17358* [*H. M. Curran*] (lectotype, designated by Jayaweera [1964: 107], NY [barcode] 00132304!; isoelectotypes, K [bc] K000740920 digital image!, US [bc] 000137843 digital image!). Figure 4.

Shrubs 1.5–5 m tall; young twigs green, densely hirsute, the trichomes more than 12-celled, brown; older branches with few to many lenticels, reddish or grayish brown, glabrous or with few scattered trichomes. Leaf blades ovate to lanceolate or ovate to elliptic, 11–30 × 5.5–12.3 cm wide, membranaceous, hirsute above, densely hirsute, especially on midrib and veins abaxially, margins ciliate, apex contracted to acuminate or caudate, not conduplicate, base attenuate or rarely obtuse; secondary veins in 10 to 14 pairs, prominulous adaxially; petioles 1–3.5 cm, densely hirsute; stipules triangular or broadly ovate, 7–12 × 3.5–7.5 mm at the base, persistent or deciduous, abaxially with dense indument, adaxially with sparse to dense hirsute apex entire or bifid 1/8 or 1/4 of length, the lobes not diverging; colleters numerous, in groups of 2 at the base. Inflorescences spreading or congested, densely hirsute; bracts numerous, lanceolate, entire, or rarely bilobed, 7–10 × 1.5–3 mm, densely hirsute underneath, glabrous above; flower pedicels 2–3.5 mm, with sparsely appressed or ascending trichomes. Flowers odorless; calyx tubes cup-shaped to shortly tubular, 2.5–4 mm, hirsute; calyx lobes linear to narrowly lanceolate, not recurved, 6–8 × 1 mm, hirsute outside, glabrous inside, occasionally with a single calycophyll; colleters 1 pair per lobe, in sinuses between calyx lobes; calycophylls with blades ovate or elliptic to ovate, 5-nerved, 5–9.4 × 3–6 cm, white, sparsely pubescent along nerves on both surfaces, margins ciliate, apex acute or acuminate, base cuneate or obtuse; calycophyll stalks 1.5–3.3 cm, densely hirsute; corolla buds hirsute, becoming sparsely hirsute only on the upper half in open flowers; corolla tubes cylindrical, forming a distinctly swollen portion around anthers, 2.2–3.5 cm long, white or greenish white, without tuft of trichomes surrounding the opening; short-styled flower morphs with dense, long, unstriated, ribbon-like trichomes internally to the base of anthers from the top; long-styled flower morphs with sparse short, striate, ribbon-like trichomes internally to the short filaments from the top; corolla lobes linear to narrowly lanceolate, 9–12(–22) × 1–1.5(–4) mm, white, abaxially hirsute, adaxially papillate; apex recurved, without filiform apical appendages; stamens inserted in the distal 1/4 of corolla in short-styled flower

morphs, inserted around middle of corolla in long-styled flower morphs, filaments glabrous, anthers linear, 3–4 mm in short-styled flower morphs, 3 mm in long-styled flower morphs, glabrous, apex obtuse; pollen diameters to 15.3 µm, apertures 4, rarely 3; ovary 3–3.5 × 1.5–2 mm, style 4–6 mm in short-styled flower morphs, 18–20(–23) mm in long-styled flower morphs, stigma 1.5–2 mm in short-styled flower morphs, 7 mm in long-styled flower morphs, smooth, recurved and included in long-styled flower morphs. Fruits ellipsoid or obovoid, 1–2 × 1–1.2 cm, with sparse to dense warts, vertical ridges slightly prominent, green, calyces deciduous or persistent, sparsely hirsute; mesocarp 0.5–0.7 mm thick; fruiting pedicels 5–8 mm, sparsely hirsute; seeds 0.67–0.83 × 0.43–0.53 mm; exotesta cells with 2 to 8 pores on inner tangential walls, tuberculate thickenings slightly prominent or inconspicuous.

Local names. Agboy (BisPn); Boyon (BisSL); Buyon (Bis), according to Alejandro (pers. obs.).

Phenology. *Mussaenda albiflora* has been collected in flower from April to November and in fruit from August to December.

Distribution and habitat. *Mussaenda albiflora* is known from Negros and Panay Islands. The species has been collected in low-altitude humid evergreen forests, on riverbanks, on roadsides, and on clay-loam soils. Its altitudinal distribution ranges from 50 to 400 m.s.m. This species is very abundant even on the roadsides of Aklan on Panay Island.

Discussion. Merrill (1910: 242) cited four collections in his protologue for *Mussaenda albiflora*, with the first two as “For. Bur. 17358 (type), 17539 Curran.” Earlier 1906 Forest Bureau collections 5539 and 5218 credited Everett and Danao and Aspillera, respectively. Jayaweera later specified *Curran 17358* in his 1964 treatment of the genus “Type” and “NY–lectotype” on pages 105 and 107, respectively. As a Philippines Forest Bureau collection, one duplicate would have been deposited at PNH and destroyed during World War II. The surviving duplicate at NY is representative of the species and was selected as lectotype, sensu Articles 9.11 and 9.12 (McNeill et al., 2012). The qualification of type in Jayaweera’s treatment of Philippine *Mussaenda* (1964: 105) was required after 1958 (cf. Arts. 40.1, 9.11, and 9.12, McNeill et al., 2012).

Mussaenda albiflora can be easily recognized by its long, linear to narrowly lanceolate corolla lobes that are pure white and the long and slender corolla tube to 3.5 cm; by the large, usually ovate to lanceolate leaves;

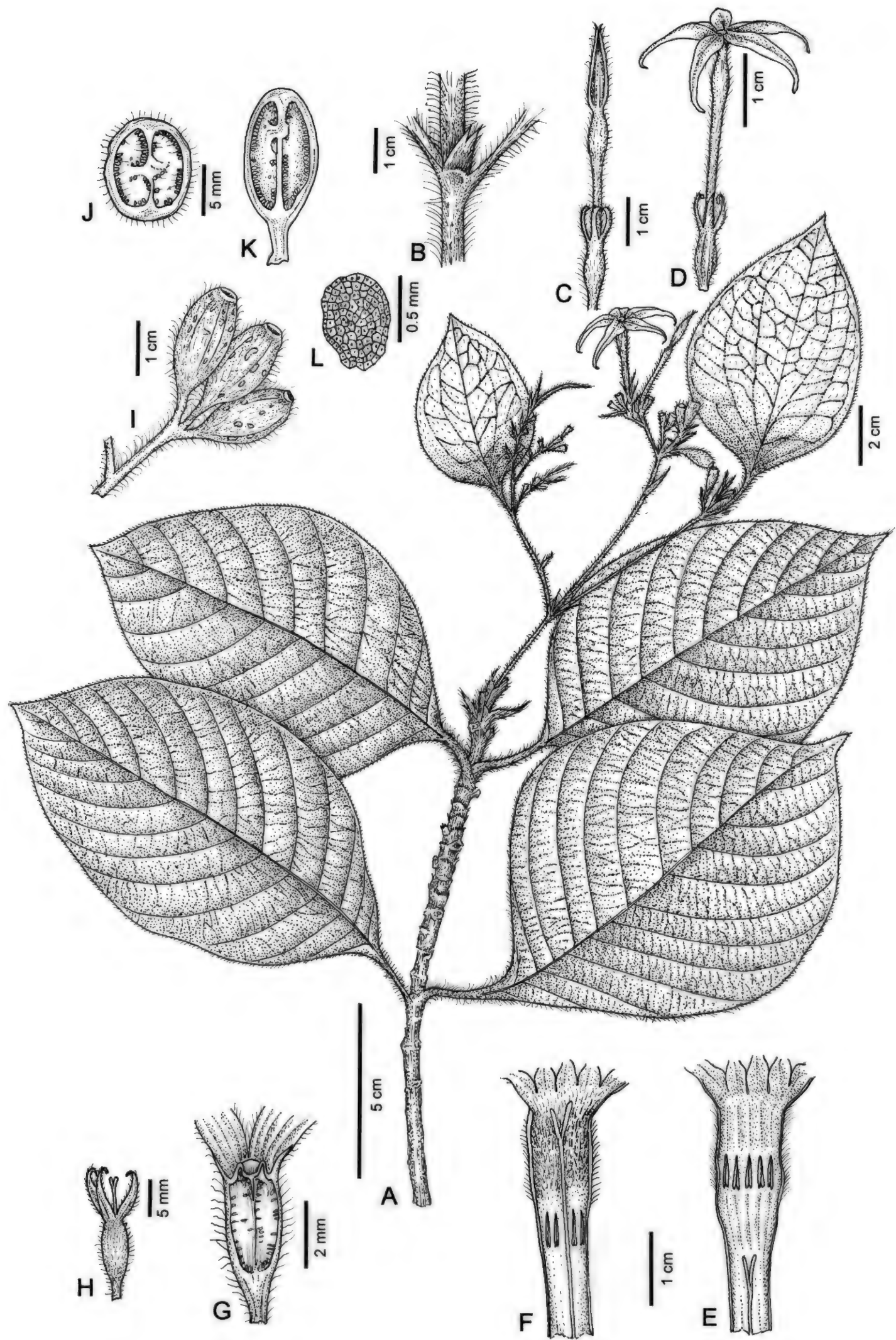


Figure 4. *Mussaenda albiflora* Merr. —A. Flowering branch. —B. Portion of stem with stipule. —C. Flower bud. —D. Open anthesal flower. —E. Short-styled flower morph, corolla tube dissected open in longitudinal section. —F. Long-styled flower morph, corolla tube dissected open in longitudinal section. —G. Longitudinal section through ovary. —H. Calyx, style, and stigma of short-styled flower morph. —I. Three fruits. —J, K. Fruit sections showing seed attachments on placentas, in cross and longitudinal sections, respectively. —L. Seed. A–E are taken from *Alejandro 30* (PNH); F–L, from *Alejandro 20* (UBT).

by the small anthers only to 4 mm in both short- and long-styled flower morphs; and by the long pedicels of the fruits, to 8 mm. It is one of the few species with long trichomes on both sides of the hirsute leaf blades, numerous bracts, recurved stigma in long-styled flower morphs, and slightly prominent vertical ridges on the fruits. *Mussaenda albiflora* resembles *M. ustii* and *M. anisophylla* in the morphology and indumentum of vegetative parts but is totally different in the structure and indumentum of reproductive parts. Both *M. albiflora* and *M. ustii* occupy the same geographical area in Panay, Aklan (Visayas), but *M. anisophylla* is found in Luzon, Mindoro, and Alabat Islands.

Additional specimens examined. PHILIPPINES. **Aklan:** Panay Island, betw. Naojon & Idio, 11°38'N, 122°06'E, *Alejandro* 43 (UBT), 046 (UBT), 50 (BR, *Univ. Santo Tomas Hb.*), 51 (L), Nabas, Mt. Laserna, 11°49'N, 122°05'E, *Alejandro* 20 (BR, UBT, *Univ. Santo Tomas Hb.*), 29 (NY, UBT, *Univ. Santo Tomas Hb.*, US), 30 (PNH, *Univ. Santo Tomas Hb.*), 31 (*Univ. Santo Tomas Hb.*), 36 (L, WAG), 37 (BM). **Antique:** [Panay Island] *McGregor* 32450 (A). **Capiz:** [Panay Island] Jamindan, 11°25'N, 122°30'E, *Ramos & Edaño* 31382 (US), Libacao, 11°28'N, 122°18'E, *Martelino & Edaño* 35391 (A, L, NY), SW range of Mt. Baloy, Musay, 3–7 km N of Lublub, 11°05'N, 122°05'E, *Varadarajan* 1531 (A, L, NY). **Iloilo:** *Reynoso et al.* 17879 (A). **Negros Occidental:** Iglamgam, 09°50'N, 122°31'E, *F. Dias* 29885 (A, NY).

3. *Mussaenda anisophylla* S. Vidal, Phan. Cuming. Philipp. 178. 1885. TYPE: Philippines. Albay: Luzon, 1841, [*H.*] *Cuming* 918 (lectotype, designated by Jayaweera [1964: 108], BM [barcode] BM000827880!; isoelectotypes, G [bc] 00436409 digital image!, K [bc] K000740919 digital image!). Figure 5.

Shrubs 2–7 m tall; young twigs green, densely hirsute, the trichomes more than 12-celled, brown; older branches with few to many lenticels, grayish white, glabrous or with few scattered trichomes. Leaf blades ovate to elliptic, 8.5–34 × 6–16 cm, membranaceous, hirsute above, densely hirsute, especially on midrib and veins underneath, margins ciliate, apex acuminate or acute to subcaudate, not conduplicate, base cuneate or attenuate; secondary veins in 7 to 15 pairs, prominulous above; petioles 1–5.5 cm, densely hirsute; stipules ovate, 7–15 × 4–8 mm at the base, deciduous, with dense indument on both sides, apex bifid 1/4 or ± half of length, the stipule lobes not diverging; colleters numerous, in continuous rows or in groups of 2 at the base. Inflorescences spreading, densely hirsute; bracts numerous, lanceolate, entire or trilobed, 6–9 × 1.5–3 mm, densely hirsute on both sides; flower pedicels 2 mm, with densely appressed or horizontal trichomes. Flowers odorless; calyx tubes cup-shaped to shortly tubular, 3–4 mm long, densely hirsute; calyx lobes

linear, not recurved, 6–15 × 1–1.5 mm, hirsute outside, glabrous or hirsute inside, occasionally with a single calycophyll; colleters in 2 pairs per lobe, in sinuses between calyx lobes; calycophylls with blades elliptic to ovate, 5-nerved, 7.5–10 × 3.2–6 cm, white, sparsely pubescent on nerves of both sides, margins ciliate, apex acute, base cuneate; calycophyll stalks 1.5–2.7 cm, densely hirsute; corolla buds densely hirsute, remaining hirsute or with few scattered trichomes in open flowers, corolla tubes cylindrical, forming a distinctly swollen portion around anthers, 2.5–3 cm long, cream, without tuft of trichomes surrounding the opening; short-styled flower morphs with unstriated, ribbon-like trichomes internally to the base of anthers from the top; long-styled flower morphs with sparse, short, striate, ribbon-like trichomes internally to the short filaments from the top; corolla lobes broadly ovate, 5–6 × 6 mm wide, orange to yellow, abaxially hirsute, adaxially papillate, apex not recurved, with or without 1-mm filiform apical appendages; stamens inserted to distal 1/4 in short-styled flower morph, inserted around middle in long-styled flower morphs, filaments glabrous, anthers linear, 5–6.5 mm in short-styled flower morphs, 4.5–5.5 mm in long-styled flower morphs, glabrous, apex acute; pollen diameter to 16.65 µm, apertures 4; ovary 3–4 × 1.5–2 mm, style 3.5–4 mm in short-styled flower morphs, 22 mm in long-styled flower morphs, stigma 2–2.5 mm in short-styled flower morphs, 9 mm in long-styled flower morphs, smooth, not recurved and included in long-styled flower morphs. Fruits ellipsoid, 1.4–2 × 0.9–1.2 cm, with few warts, vertical ridges absent, green, sparsely hirsute, calyces persistent or deciduous; mesocarp 0.4–0.7 mm thick; fruiting pedicels 3–4 mm long, sparsely hirsute; seeds 0.63–0.73 × 0.33–0.63 mm; exotesta cells with 2 to 6 pores on the inner tangential walls, tuberculate thickenings slightly prominent or inconspicuous.

Local names. Ayon-a-kilat (Mar); Bodas (Igt); Buyon (Bis); Gagat, Gulugulpu, Kalkalpu (Ifg); Kahoy-dalaga (Tag); Mabiyn (Bng); Quiitogon (Kal); Talig-harap, Tinga-tinga (Tag), according to Alejandro (pers. obs.).

Phenology. *Mussaenda anisophylla* has been collected in flower from January to July and September to November, and in fruit from January to February, May to June and November to December.

Distribution and habitat. *Mussaenda anisophylla* has been found on Luzon, Mindoro, and Alabat Islands. It has been collected in low- or mid-altitude forests or from mossy forests, shaded ravines, streamsides, and on clay or sandy soils. Its known altitudinal extent is 100–800 m.s.m.

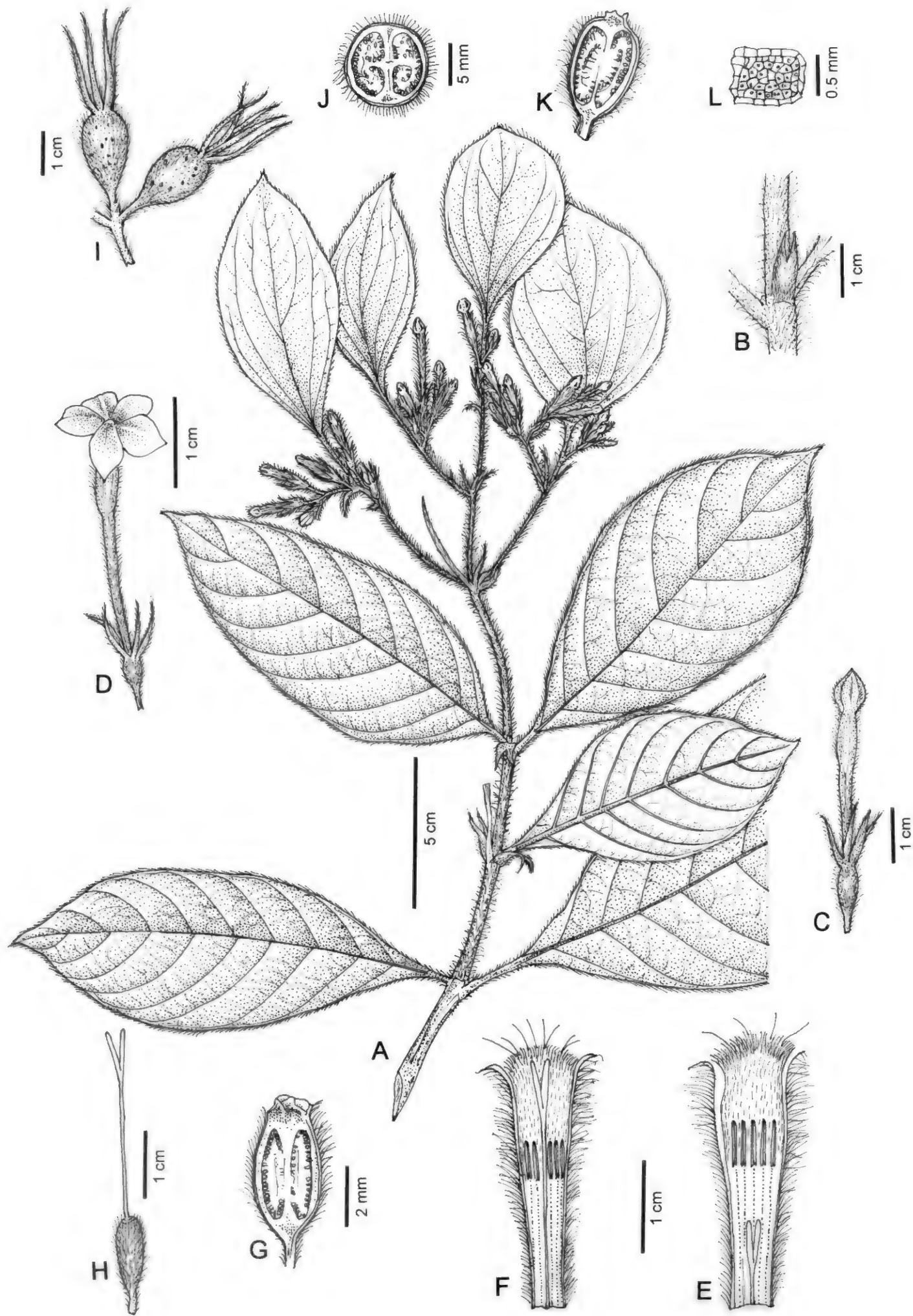


Figure 5. *Mussaenda anisophylla* S. Vidal. —A. Flowering branch. —B. Portion of stem with stipule. —C. Flower bud. —D. Open anthesal flower. —E. Short-styled flower morph, corolla tube dissected open in longitudinal section. —F. Long-styled flower morph, corolla tube dissected open in longitudinal section. —G. Longitudinal section through ovary. —H. Calyx, style, and stigma of long-styled flower morph, with the corolla and calyx lobes removed. —I. Two fruits with persistent calyces. —J, K. Fruit sections showing seed attachments on placentas in cross and longitudinal sections, respectively. —L. Seed. A–E are taken from *Celestino* 7819 (PNH); F–H, from *Edaño* 3500 (L); I–L, from *Sulit* 7087 (PNH).

Discussion. Vidal (1885: 178) cited only the single collection “Cum. 918 Prov. Albay” in his description of *Mussaenda anisophylla*. Jayaweera (1964: 108) would later cite *Cuming 918* as “TYPE,” also noting the collection as “BM–lectotype.” As a Forest Bureau collection for the Philippines, one duplicate would have been deposited at PNH and was lost during World War II with the destruction of the herbarium. The surviving duplicate at BM is representative of the species, noted as type (sensu Art. 40.1) and lectotype (cf. Arts. 9.11 and 9.12, McNeill et al., 2012) by Jayaweera.

Jayaweera (1964) mistakenly annotated most fruiting specimens of *Mussaenda anisophylla* as *M. philippinensis*. Based on the fruits, the two species are strikingly disparate. The fruits of *M. anisophylla* are generally ellipsoid, larger to 2×1.2 cm, warty, sparsely hirsute, and with shorter, deciduous or persistent calyces. In *M. philippinensis*, the fruits are globose or ellipsoid, smaller to 1.5×0.8 cm, smooth, densely hirsute, and with the calyces always persistent and longer. *Mussaenda anisophylla* resembles *M. magallanensis* and *M. albiflora* based on the hirsute indument of vegetative and reproductive organs. However, *M. anisophylla* is characterized by longer leaf petioles to 3.5 cm, deeply bifurcate stipules, longer calyx lobes to 8 mm, larger calycophylls to 9.4×6 cm, densely hirsute inflorescence axes, wider corolla lobes to 6 mm, and with a denser hirsute indumentum before anthesis.

Additional specimens examined. PHILIPPINES. **Albay:** Bicol region, Brgy. Bulang, Mt. Malinao, $13^{\circ}10'N$, $123^{\circ}25'E$ (*Univ. Santo Tomas Hb.*). **Bataan:** Lamao river, Mt. Marivales, $14^{\circ}31'N$, $120^{\circ}29'E$, *Merrill 2508* (A, MO, NY, PNH, US), *Meyer 3020* (NY), *Borromeo 25602* (US). **Batangas:** *Vidal 801* (A). **Ifugao:** $16^{\circ}50'N$, $121^{\circ}10'E$, *Conklin & del Rosario 72628* (PNH). **Kalinga:** Lubuagan, Mabuntot, $17^{\circ}20'N$, $121^{\circ}11'E$, *del Rosario & Cordero 96180* (PNH, US); Balbalan, $17^{\circ}25'N$, $121^{\circ}11'E$, *Celestino 7819* (A, PNH). **Laguna:** Luzon Island, Los Banos, Mt. Makiling, $14^{\circ}10'N$, $121^{\circ}13'E$, *Canicosa 9730* (PNH), *Elmer 17481* (A, MO, NY), *Stern 2185* (L, PNH), *Sulit 7087* (A, PNH), *8232* (PNH). **Mindoro [Occidental]:** Paluan, $13^{\circ}25'N$, $120^{\circ}28'E$, *Ramos 39509* (US); Mt. Ilong, *Edaño 373* (PNH), *Edaño 3290* (A); Mt. Halcon, $13^{\circ}15'N$, $120^{\circ}59'E$, *Edaño 3500* (L, MO), *114* (PNH), *Edaño & Ramos 40589* (PNH, US), *Ramos & Edaño 40703* (A); Sabang River, $13^{\circ}30'N$, $120^{\circ}58'E$, *Reed 93778* (PNH); Lauaan, Abra de Ilog, $13^{\circ}26'N$, $120^{\circ}44'E$, *Sulit 13813* (PNH); vic. Puerto Galera, *Bartlett 13459* (A). **Mountain:** Banaue, Amganad, Brgy. Bulang, $16^{\circ}53'N$, $121^{\circ}04'E$, *Banluga 72607* (PNH), Mt. Hagada, Brgy. Pula, $16^{\circ}52'N$, $121^{\circ}54'E$, *Reynoso et al. 14506* (A). **Nueva Viscaya:** Dupax, $16^{\circ}17'N$, $121^{\circ}04'E$, *Merrill 299* (US). **Pangasinan:** Labrador, Mt. San Isidro, $16^{\circ}01'N$, $120^{\circ}09'E$, *Fenix 29851* (NY). **Quezon:** Alabat Island, *Merrill 10437* (A, L, PNH, US), *Ramos & Edaño 48110* (NY); Tayabas, Lucban, $14^{\circ}07'N$, $121^{\circ}33'E$, *Elmer 9154* (MO, NY, US), Mt. Binuang, $14^{\circ}55'N$, $121^{\circ}55'E$, *Ramos & Edaño 28783*

(A), *28687* (A), Mt. Tulaog, $14^{\circ}46'N$, $121^{\circ}37'E$, *Ramos & Edaño 29093* (A). **Zambales:** *Ramos 5044* (NY).

4. *Mussaenda attenuifolia* Elmer, Leaflet. Philipp. Bot. 5: 1875. 1913. TYPE: Philippines. Agusan del Norte: Mindanao, Cabadbaran, Mt. Urdaneta, $09^{\circ}07'N$, $125^{\circ}33'E$, July 1912, A. D. E. *Elmer 13304* (lectotype, designated by Jayaweera [1964: 110], A [barcode] 00096195!; isolectotypes, BISH [bc] 1004481 digital image!, BRIT [bc] 23828 digital image!, CAS [bc] 0007108 digital image!, E [bc] 00502294 digital image!, GH [bc] 00096194 digital image!, K [bc] K000740918 digital image!, L!, MO [bc] 000716845!, NY [bc] 00132305!, U [bc] 0117320 digital image!, US [bc] 001051173!).

Shrubs 5 m tall; young twigs greenish brown, densely pubescent, the trichomes less than 12-celled, brown; older branches lenticellate, grayish white, glabrous. Leaf blades oblanceolate or elliptic, $7\text{--}20 \times 3.5\text{--}6.7$ cm, membranaceous, sparsely pubescent above, densely pubescent especially on midrib and veins underneath, margins ciliate, apex acuminate or subcaudate, not conduplicate, base attenuate; secondary veins in 10 to 14 pairs, prominulous above; petioles 0.5–1.5 cm, densely pubescent; stipules triangular or ovate, $5\text{--}11 \times 4.5\text{--}5.5$ mm at the base, deciduous, with dense indument on both sides; apex bifid \pm half of length, the stipule lobes not diverging; colleters numerous, in continuous rows at the base. Inflorescences spreading, densely pubescent; bracts few, linear to narrowly lanceolate, entire, $5\text{--}8 \times 1\text{--}2.8$ mm, densely pubescent underneath, pubescent above; flower pedicels 1–1.5 mm, with sparse appressed trichomes. Flowers odorless; calyx tubes cup-shaped to shortly tubular, 3–4.5 mm, densely pubescent; calyx lobes lanceolate, not recurved, $3 \times 0.8\text{--}1.2$ mm, pubescent on both sides, occasionally with a single calycophyll; colleters as 1 or 2 pairs per lobe, in sinuses between calyx lobes; calycophylls with blades ovate or elliptic to ovate, 5-nerved, $8\text{--}13 \times 5\text{--}8$ cm, white or cream, sparsely pubescent along nerves of both sides, margins ciliate, apex acuminate, base attenuate; calycophyll stalks 2–3 cm, densely pubescent; corolla buds densely pubescent, remaining pubescent or only in upper half and with few scattered trichomes below in open flowers; corolla tubes cylindrical, forming a distinctly swollen portion around anthers, 2.7–4 cm long, yellowish white, with tuft of trichomes surrounding the opening; long-styled flower morphs with sparse short, striate, ribbon-like trichomes internally to base of anthers or to the short filaments from the top; short-styled flower morphs not seen; corolla lobes ovate or broadly elliptic, $4\text{--}5 \times$

2.5–4 mm, orange to yellow, abaxially pubescent, adaxially papillate, apex not recurved, with or without 1-mm filiform apical appendages; stamens inserted around middle in long-styled flower morphs, filaments glabrous, anthers linear, 4–5 mm in long-styled flower morphs, glabrous, apex obtuse; pollen diameter to 15.75 μm , apertures 4; ovary 3–3.5 \times 2–2.5 mm, style 18 mm in long-styled flower morphs, stigma 7.5–8 mm, smooth, not recurved, included in long-styled flower morphs. Fruits ellipsoid to obovoid, 1.2–2 \times 0.9–1 cm, smooth, with slightly prominent vertical ridges, green, calyces deciduous, sparsely pubescent; mesocarp 0.3–0.5 mm thick; fruiting pedicels 4–6 mm, sparsely pubescent; seeds 0.64–0.77 \times 0.43–0.63 mm; exotesta cells with 2 to 6 pores on inner tangential walls, tuberculate thickenings absent.

Local names. Bungog (Mbo); Buway (Bgb), according to Alejandro (pers. obs.).

Phenology. The collector of the type, Elmer, collected flowers and fruits in July 1912.

Distribution and habitat. *Mussaenda attenuifolia* is endemic to the southernmost island group of Mindanao, from the province of Agusan del Norte. It has been collected from low- and mid-altitudes on Mount Urdaneta, along creeksides, from altitudes of 150–450 m.s.m. This species appears to have a restricted distribution on Mount Urdaneta, Mindanao, and has not been re-collected since 1912.

Discussion. Elmer (1913: 1875) cited his “Type specimen number” as 13304, and Jayaweera (1964: 110) would later specify “A–lectotype; GH, NY, US–isotypes.” Additional isoelectotypes (BISH, BRIT, CAS, E, K, L, MO, and U) have been found, although Elmer’s type at PNH was destroyed, along with the herbarium during World War II.

Jayaweera (1964) regarded this species as closely related to *Mussaenda palawanensis* based on the morphology of stipules, shape of corolla lobes, and number of seed perforations. However, the two species are characterized by remarkable differences based on these similarities. *Mussaenda attenuifolia* has smaller, triangular or ovate, not diverging stipules, and shorter, ovate or elliptic corolla lobes to 5 mm long, with short filiform appendages to 1 mm. In contrast, *M. palawanensis* is marked by larger, triangular, sometimes diverging stipules, and longer, ovate corolla lobes to 10 mm long with long filiform appendages to 2.5 mm. *Mussaenda attenuifolia* is rather distinctive by its large calycophylls, which are

strictly attenuate at the base, by its corolla tubes to 4.5 mm long, and by the smooth surfaces of its fruits.

5. *Mussaenda benguetensis* Elmer, Leaf. Philipp. Bot. 1: 13. 1906. TYPE: Philippines. Benguet: Luzon, Baguio, 16°24'N, 120°35'E, Mar. 1904, A. D. E. Elmer 5935 (lectotype, designated here, NY [barcode] 00132306!; isoelectotypes, K [bc] K000740917 digital image!, US [bc] 000137845 digital image!). Figure 6.

Shrubs or trees, 1–5 m tall; young twigs greenish brown, sparsely to densely hirsute, the trichomes more than 12-celled, brown; older branches with few lenticels, reddish or grayish brown, with few scattered trichomes. Leaf blades ovate to elliptic or lanceolate, 6–11 \times 3–5 cm, subcoriaceous, sparsely pubescent above, densely pubescent, especially on the midrib and veins underneath, margins ciliate, apex acute or acuminate to subcaudate, not conduplicate, base cuneate or obtuse; secondary veins in 8 to 11 pairs, prominulous above; petioles 0.5–2 cm, densely hirsute; stipules broadly oblong or ovate, 7–10 \times 6.8–9 mm at the base, persistent, abaxially with dense indument, adaxially with sparse indument only at the base; apex bifid \pm half to 3/4 length, the stipule lobes distinctly diverging; colleters numerous, in groups of 2 at the base. Inflorescences congested, densely hirsute; bracts few, lanceolate, entire to trilobed, 4–13 \times 0.7–2 mm, densely pubescent underneath, glabrous or sparsely pubescent above; flower pedicels 1–2 mm, with densely appressed trichomes. Flowers rarely 6-merous, sweet-scented; calyx tubes cup-shaped to shortly tubular, 4–7 mm, densely pilose; calyx lobes subulate, not recurved, 9–10 \times 2 mm, pilose on both surfaces, occasionally with a single calycophyll; colleters as 2 to 4 pairs per lobe, in sinuses between calyx lobes or in a row at the base adaxially; calycophylls with blades ovate or elliptic to ovate, 5-nerved, 3–5.2 \times 2–4 cm, white, sparsely pubescent along nerves of both surfaces, margins ciliate, apex acuminate, base attenuate; calycophyll stalks 0.4–0.8 cm, densely pilose; corolla buds densely pilose, variably pilose in open flowers; corolla tubes infundibular, the swollen portion around anthers indistinct, 3–3.7 cm long, yellowish or greenish white, with tuft of trichomes surrounding the opening; in short-styled flower morphs with dense, long, unstriate, ribbon-like trichomes internally to the base of anthers or to the short filaments from the top; in long-styled flower morphs with mixed or alternating variably globular trichomes and short, verrucose, straplike trichomes internally to the short filaments from the top; corolla lobes ovate or broadly elliptic, 5–8 \times 4–6 mm, yellow, abaxially pilose, adaxially papillate, apex recurved or not, with or without 1.5-mm filiform apical appendages; stamens inserted to

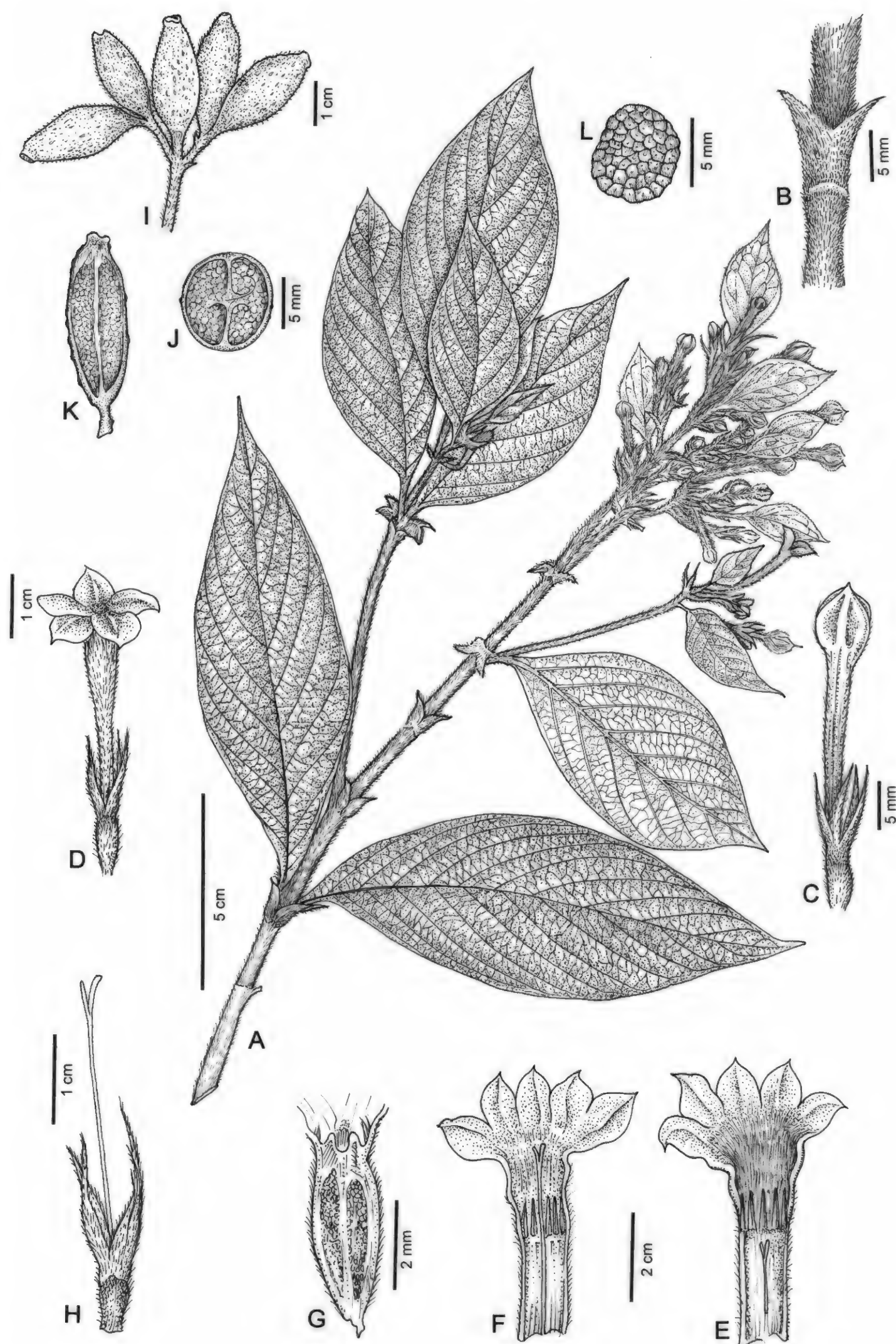


Figure 6. *Mussaenda benguetensis* Elmer. —A. Flowering branch. —B. Portion of stem with stipule. —C. Flower bud. —D. Open anthesal flower. —E. Short-styled flower morph, corolla tube dissected open in longitudinal section. —F. Long-styled flower morph, corolla tube dissected open in longitudinal section. —G. Longitudinal section through ovary. —H. Calyx, style, and stigma of long-styled flower morph, with the corolla removed. —I. Five fruits. —J, K. Fruit sections showing seed attachments on placentas, in cross and longitudinal sections, respectively. —L. Seed. A–D are taken from Conklin & del Rosario 72703 (PNH); E, from Alejandro 110 (Univ. Santo Tomas Hb.); F–L, from Alejandro 108 (UBT).

distal 1/4 in short-styled flower morphs, around middle or to distal 1/4 in long-styled flower morphs, filaments glabrous, anthers linear, 5–6 mm in short-styled flower morphs, 5–5.5 mm in long-styled flower morphs, glabrous, apex acute or obtuse; pollen diameters to 19.8 μm , apertures 4, rarely 3; ovary 3.5–4.5 \times 2–2.5 mm, style 4–7 mm in short-styled flower morphs, 22–25 mm in long-styled flower morphs; stigma 2–3 mm in short-styled flower morphs, 5–6.5 mm in long-styled flower morphs, smooth, not recurved and included in long-styled flower morphs. Fruits narrowly ellipsoid, 2–3 \times 0.6–0.9 cm, with dense warts, without vertical ridges, brown, sparsely pubescent, calyces deciduous; mesocarp 0.3–0.5 mm thick; fruiting pedicels 2–4 mm, densely pubescent; seeds 0.7–0.77 \times 0.53–0.63 mm; exotesta cells with 4 to 9 pores on the inner tangential walls, tuberculate thickenings slightly prominent.

Local names. Bilaw (Igt); Elado, Gelido, Kalkalpu (Ifg); Otoy-otoy (Igt); Salimaguok (Tng); Sangsang, Ugwa-ugwa (Igt); Wuguawugua (Bon), according to Alejandro (pers. obs.).

Phenology. *Mussaenda benguetensis* has been observed to flower from January to June, August, and October to December, and in fruit from January to February, June, and October to December.

Distribution and habitat. *Mussaenda benguetensis* is known from Ifugao, Benguet, and Mountain Provinces on Luzon Island. It has been collected from secondary or primary forests, along roadsides, on ravines, from loamy or sandy soils, and from elevations ranging from 300 to 2300 m.s.m.

Discussion. Although documented by Jayaweera (1964: 112), the PNH holotype of *Mussaenda benguetensis* was not encountered in the recent investigation of Rubiaceae types at PNH and is presumed to have been destroyed during World War II. Therefore, the isotype of *M. benguetensis* at the NY herbarium is here designated as the lectotype, and isoelectotypes in K and US have also been found.

Mussaenda benguetensis is distinct from other Philippine *Mussaenda* species by its prominently diverging, broadly oblong or ovate stipules; by its small, crowded leaves 6–11 cm long; by its sweet-scented flowers, with mixed or alternating globular and strap-shaped trichomes inside the corolla tubes in long-styled flower morphs; and by the narrowly ellipsoid fruits to 3 cm long. Like *M. benguetensis*, both *M. chlorantha* and *M. lanata* are also found in Benguet, Ifugao, and Mountain Provinces of Luzon. However, *M. benguetensis* differs from the other two based on its distinct features.

Additional specimens examined. PHILIPPINES. **Benguet:** Tuba, Cabuyao, Mt. Sto. Tomas, 16°23'N, 120°33'E, *Alejandro 108* (UBT), *111* (PNH, Univ. Santo Tomas Hb.), *Elmer 6536* (NY), *Garcia 34977* (PNH), *Quisumbing 2193* (PNH), *Sinclair & Edaño 55365* (PNH), *9689* (L, PNH, US), *Steiner 267* (US); Baguio, 16°24'N, 120°35'E, *Clemens 51845* (A, US), *Elmer 8431* (A, NY), *9535* (PNH), *Steiner 22585* (PNH), *35835* (PNH), *41617* (PNH), *Topping 64* (US), *Valbuena & Lopez 91899* (PNH), *Walker 7501* (US), *Williams 1006* (A, NY); Kabayan, Mt. Libbung, 16°38'N, 120°50'E, *Mendoza 40936* (PNH); Papuai, *Santos 31880* (NY), *Santos 34* (A, MO); Mt. Pulog, 16°36'N, 120°54'E, *Alejandro 110* (PNH, Univ. Santo Tomas Hb.), *Mendoza 104012* (PNH). **Ifugao:** Luzon Island, Banaue, Bayninnan, 17°11'N, 120°45'E, *Conklin & Buwaya 80640* (PNH); Sumigar, *Conklin & del Rosario 72703* (A, L, PNH); Mt. Polis, 16°48'N, 121°07'E, *Alejandro 107* (BR, L, NY, WAG), *Steiner 41580* (PNH, US). **Mountain:** Bontoc, Besao, Barrio Agawa, 17°04'N, 120°52'E, *Santos 5497* (US); Mt. Nangaoto, *Sulit 7722* (BR, PNH).

6. *Mussaenda chlorantha* Merr., Philipp. J. Sci. 8(Pt. C): 47. 1913. TYPE: Philippines. Benguet: Luzon Island, Mt. Tonglon, 16°23'N, 120°38'E, May 1911, *E. D. Merrill 770* (lectotype, designated by Jayaweera [1964: 113], US [barcode] 001310695!; isoelectotypes, FR [bc] 0030824 digital image!, M [bc] 0198427 digital image!, U [bc] 0041553 digital image!). Figure 7.

Trees 5–8 m tall; young twigs green, pilose, trichomes less than 12-celled, brown; older branches with few to many lenticels, reddish or grayish brown, glabrous. Leaf blades broadly ovate, 10–18 \times 5–12 cm, subcoriaceous, sparsely pubescent on both surfaces, especially on midrib and veins underneath, margins ciliate, apex shortly acuminate, not conduplicate, base cuneate or attenuate; secondary veins in 7 to 13 pairs, prominulous above; petioles 1.5–4 cm, pubescent; stipules ovate or triangular, 7–10 \times 3.5–6.5 mm at the base, persistent or deciduous, with dense pilose indument on both sides; apex entire or bifid 1/4 length, the stipule lobes not diverging; colleters numerous, in continuous rows or in groups of 2 at the base. Inflorescences spreading, densely pilose; bracts few, linear-lanceolate or ovate-lanceolate, entire or trilobed, 4–8 \times 1.5–3 mm, densely pubescent underneath, pubescent above; flower pedicels 1.5–2 mm, with densely appressed trichomes. Flowers odorless; calyx tubes cup-shaped to shortly tubular, 5 mm long, densely pilose; calyx lobes lanceolate or subulate, not recurved, 8–10 \times 2–2.5 mm, pilose on both surfaces, occasionally with a single calycophyll; colleters 1 pair per lobe, in sinuses between calyx lobes; calycophylls with blades broadly ovate, 5-nerved, 5–8 \times 3.5–5 cm, white, sparsely pubescent along nerves on both surfaces, margins ciliate, apex acute or acuminate, base cuneate; calycophyll stalks 1.5–2 cm, densely pilose; corolla buds and open flowers densely pilose;

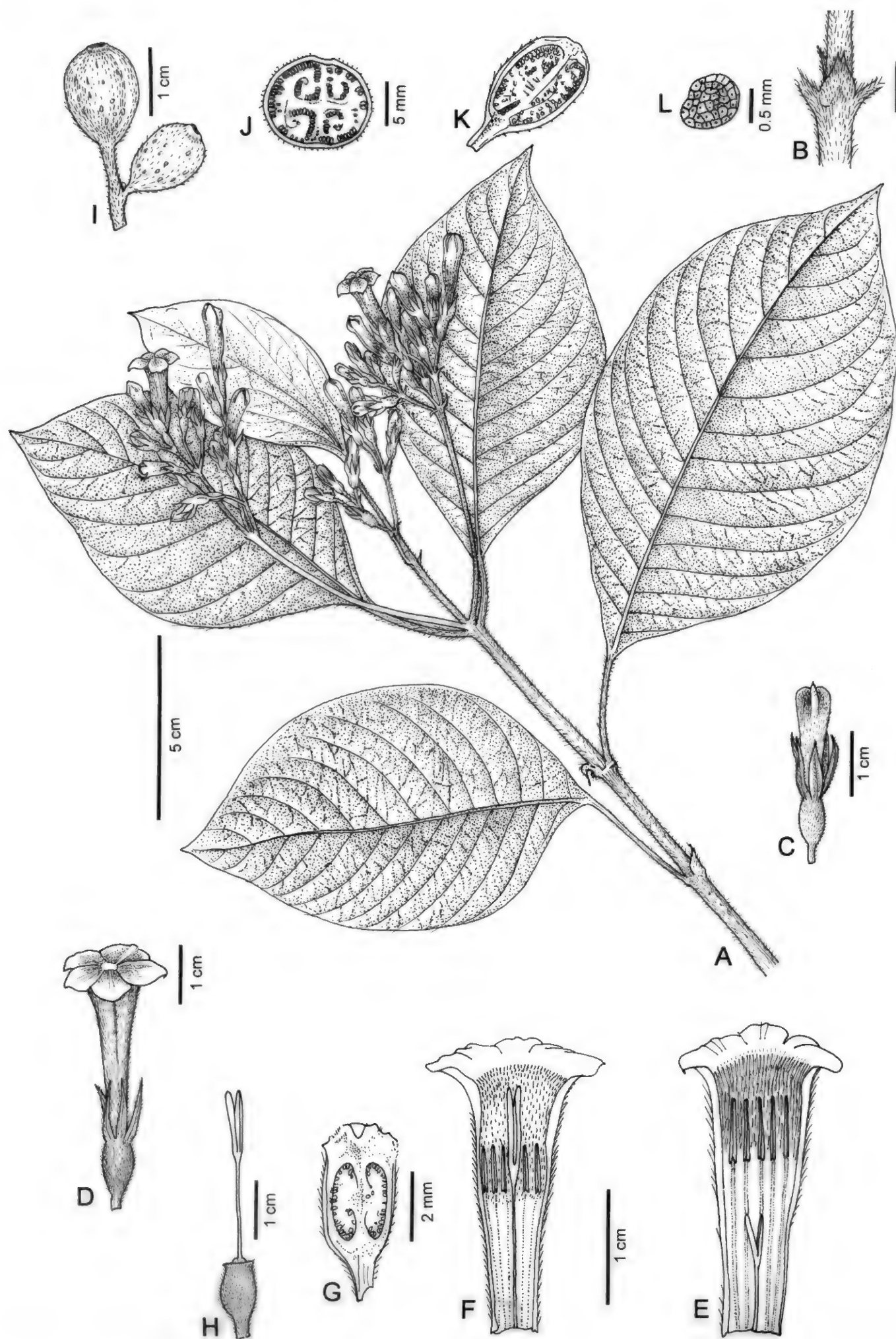


Figure 7. *Mussaenda chlorantha* Merr. —A. Flowering branch. —B. Portion of stem with stipule. —C. Flower bud. —D. Open anthesal flower. —E. Short-styled flower morph, corolla tube dissected open in longitudinal section. —F. Long-styled flower morph, corolla tube dissected open in longitudinal section. —G. Longitudinal section through ovary. —H. Calyx, style, and stigma of long-styled flower morph, with the corolla and calyx lobes removed. —I. Two fruits. —J, K. Fruit sections showing seed attachments on placentas, in cross and longitudinal sections, respectively. —L. Seed. A–E are taken from Santos 31725 (NY); F–L, from Alejandro 109 (UBT).

corolla tubes infundibular, swollen portion around anthers indistinct, 2–2.3 cm, brownish green, without tuft of trichomes surrounding the opening; short-styled flower morphs with dense, long, unstriated, ribbon-like trichomes internally to the base of anthers from the top; long-styled flower morphs with sparse short, striate, ribbon-like trichomes internally to the short filaments from the top; corolla lobes ovate or broadly elliptic, 4–5 × 5–6 mm, orange or yellow, abaxially pilose, adaxially papillate; apex not recurved, without filiform apical appendages; stamens inserted to distal 1/4 in short-styled flower morphs, around middle in long-styled flower morphs, filaments glabrous, anthers linear, 5–6 mm in short-styled flower morphs, 4.5–5 mm in long-styled flower morphs, glabrous or with few scattered trichomes, apex acute or obtuse; pollen diameters to 16.2 μ m, apertures 4; ovary 3–3.5 × 1.5–2.5 mm, style 5 mm in short-styled flower morphs, 15–17 mm in long-styled flower morphs, stigma 1.5 mm in short-styled flower morphology, 7–8 mm, smooth, not recurved and included in long-styled flower morphs. Fruits obovoid, 1–1.4 × 0.9–1.1 cm, with sparse warts, without vertical ridges, green, calyces deciduous, glabrous or with few scattered hairs; mesocarp 0.4–0.6 mm thick; fruiting pedicels 3–3.5 mm, glabrous or sparsely pubescent; seeds 0.7–0.83 × 0.5–0.56 mm, exotesta cells with 4 to 12 pores on the inner tangential walls, tuberculate thickenings absent.

Local names. Buyon (Bis); Buyon-kahoy (Tag), according to Alejandro (pers. obs.).

Phenology. *Mussaenda chlorantha* has been observed to flower in February, April to June, and October to November, and in fruit from October to November.

Distribution and habitat. *Mussaenda chlorantha* is known from Luzon Region/Island, from Rizal, Pampanga, Ifugao, Benguet, and Mountain Provinces, and to the south in the Visayas Islands, from Negros Oriental Province. It has been collected in mid- to high-altitude evergreen forests, from ravines, on riverside banks, on clay-loamy soils, and from elevations of 400–2040 m.s.m.

Discussion. Merrill mentioned only the one collection *Merrill 770* in his 1913 protologue, the holotype of which was destroyed at PNH during World War II. Jayaweera (1964: 113) identified a surviving duplicate at US as “lectotype,” and the authors have seen other duplicates (FR, M, and U) that are designated here as isolectotypes.

Merrill (1913) and Jayaweera (1964) regarded *Mussaenda chlorantha* as closely similar to *M.*

macrophylla Wall., but did not mention particular similarities between the two species. In terms of the indumentum, size, and shape of reproductive structures, the two species are vastly dissimilar. *Mussaenda chlorantha* rather resembles *M. lanata* in the form of the corolla bud. However, *M. chlorantha* has a different indumentum type (pilose vs. hirsute in *M. lanata*) and obviously longer corolla tubes of a different color (to 2.3 cm and brownish green vs. 1.5 cm and yellowish white). Other distinctive characters of *M. chlorantha* include the broadly ovate leaves, ovate corolla lobes, and strict tree habit. This species is common and can be expected from other provinces on Luzon Island, extending southward to Negros Oriental in the Visayas Island group.

Additional specimens examined. PHILIPPINES. **Benguet:** Benguet, Tuba, Cabuyao, Mt. Sto. Tomas, 16°23'N, 120°34'E, *Alejandro 109* (UBT, *Univ. Santo Tomas Hb.*); Pauai, *Santos 31725* (L, NY); Twin Peaks, *Elmer 6318* (NY), *6381* (US). **Ifugao:** Mt. Polis, 16°48'N, 121°07'E, *Celestino 7879* (L). **Mountain:** Bontoc, 17°04'N, 120°58'E, *Vanoverbergh 190* (A, L, MO). **Negros Oriental:** Dumaguete, Mt. Cuernos, 09°18'N, 123°18'E, *Elmer 9966* (A, MO, NY). **Pampanga:** Camp Stotsenburg, Mt. Pinatubo, 15°09'N, 120°32'E, *Elmer 21940* (MO, NY, PNH). **Rizal:** Luzon, Mt. Irig, 14°36'N, 121°11'E, *Ramos 42135* (BR).

7. *Mussaenda grandibracteata* Alejandro, sp. nov.

TYPE: Philippines. Occidental Mindoro: Mag-saysay, San Nicolas, 12°21'N, 121°06'E, 15 Oct. 2002, *G. J. D. Alejandro & J. C. Castro 14* (holotype, PNH!; isotypes, NY [barcode] 006888885!, *Univ. Santo Tomas Hb.*!). Figure 8.

Haec species ab aliis speciebus generis bracteis et bracteolis numerosis grandibus luteoviridibus, stipulis integris vel breviter bifidis et tubo calycis brevissimo differt.

Shrubs 1.5–3 m tall; young twigs greenish brown, glabrous; older branches with few to many lenticels, reddish or grayish brown, glabrous. Leaf blades elliptic to widely obovate, 7–22.5 × 3.2–10.3 cm, membranaceous, glabrous above, with few scattered minute trichomes underneath, margins glabrous, apex acute or acuminate, not conduplicate, base cuneate or long attenuate, secondary veins in 9 to 11 pairs, prominent above; petioles 0.4–3.5 cm, glabrous; stipules ovate, 7–9 × 4–5.5 mm at the base, deciduous, abaxially pubescent, adaxially with dense indument only at the base; apex entire or bifid 1/8 of length, the stipule lobes not diverging; colleters numerous, in groups of 2 at the base. Inflorescences spreading or congested, glabrescent; bracts and bracteoles numerous, about 10 or more per inflorescence axes, yellow-green, lanceolate, entire or trilobed, 7–13 × 2.5–5 mm,



Figure 8. *Mussaenda grandibracteata* Alejandro. —A. Flowering branch. —B. Portion of stem with stipules. —C. Flower bud. —D. Open anthesal flower. —E. Short-styled flower morph, corolla tube dissected open in longitudinal section (long-styled flower morph not seen). —F. Longitudinal section through ovary. —G. Calyx, style, and stigma of short-styled flower morph, with the corolla and calyx lobes removed. A–G from the type *Alejandro & Castro 14* (PNH).

sparsely pubescent underneath, glabrous or sparsely pubescent above; flower pedicels 1.5–2 mm, glabrous or with few scattered trichomes. Flowers odorless; calyx tubes, 1.5–2.5 mm long, glabrescent; calyx lobes linear to lanceolate, not recurved, $7\text{--}10 \times 1\text{--}1.5$ mm, pubescent on both sides, occasionally with a single calycophyll; colleter as 1 pair per lobe, in sinuses between calyx lobes, or sometimes absent; calycophylls with blades elliptic, 5-nerved, $5.5\text{--}7.4 \times 3.2\text{--}4.8$ cm, white or cream, glabrous above, glabrous or pubescent only along nerves beneath, margins glabrous, apex acute or acuminate, base cuneate; calycophyll stalks 1.5–2 cm, glabrous or with few scattered short trichomes; corolla buds puberulous, becoming glabrous or with few scattered trichomes in open flowers; corolla tubes cylindrical, forming a distinctly swollen portion around anthers, 2.2–2.4 cm long, yellowish green, with tuft of trichomes surrounding the opening; short-styled flower morphs with dense, long, unstriate, ribbon-like trichomes internally to the base of anthers from the top; long-styled flower morphs not seen; corolla lobes ovate to elliptic, $3\text{--}3.5 \times 3\text{--}4$ mm, yellow or yellow-orange, abaxially glabrous or puberulous, adaxially papillate, apex not recurved, without filiform apical appendages; stamens inserted to distal 1/4 in short-styled flower morphs, filaments glabrous, anthers linear, 3–4.5 mm in short-styled flower morphs, glabrous, apex acute; pollen diameters to $15.75\text{ }\mu\text{m}$, apertures 4; ovary $1.5\text{--}2.4 \times 1.5\text{--}2$ mm, style 3–5 mm in short-styled flower morphs; stigma 1–2 mm in short-styled flower morphs, smooth. Fruits not seen.

Local name. Banay-dagat (Myn), according to Alejandro (pers. obs.).

Etymology. The specific epithet of the new species refers to its large bracts.

Phenology. *Mussaenda grandibracteata* was observed to flower from September to November, but fruits were not seen.

Distribution and habitat. *Mussaenda grandibracteata* has been collected from the province of Mindoro Occidental in the central Philippines and from the province of Davao del Sur to the south in the Mindanao Region. A geographical disjunction is obvious, but probably this species can be found also in the intervening provinces. The new species is known from low-altitude secondary and primary forests, on slopes near the road, on sandy or ultramafic soils, at altitudes from 25 to 300 m.s.m. The Philippine Plant Inventory Team (PPIT) of the PNH herbarium recently botanized the locality and found the type specimen (Mindoro Occidental: San Nicolas).

IUCN Red List category. *Mussaenda grandibracteata* is assessed as Endangered or EN, C2a(i), according to IUCN (2001) criteria. The population size is estimated to number fewer than 2500 mature individuals. A continuing decline is projected, with no subpopulation estimated to contain more than 250 mature individuals or even more than 50. Suitable habitats for *M. grandibracteata* are threatened by human land use in Magsaysay (Mindoro Occidental) and are threatened by human activity, as one subpopulation is located on the much visited Mount Apo (Davao del Sur).

Discussion. *Mussaenda grandibracteata* is distinguished by having numerous, large, yellow-green bracts that subtend the flowers, by the entire or shortly bifid apices of the stipules, and by the much reduced calyx tubes only to 2.5 mm long. This species is somewhat similar to *M. magallanensis* in the morphology of the leaves and flowers. However, the vegetative and reproductive parts of *M. grandibracteata* are more or less glabrous, whereas in *M. magallanensis* these parts are densely hirsute. *Mussaenda scandens* is the only other Philippine species that has comparably short calyx tubes to 1.8–2.5 mm, and glabrescent young twigs and inflorescences. *Mussaenda grandibracteata* differs from *M. scandens* by its non-conduplicate leaf apices, minimal bifurcation of stipules to one eighth of their length, numerous and wider bracts, and long calyx lobes to 7–10 mm. Both species occur on Mount Apo of Davao del Sur, but *M. grandibracteata* extends to Mindoro Occidental, while *M. scandens* is strictly distributed in the provinces of Mindanao.

Paratypes. PHILIPPINES. **Davao del Sur:** Mindanao, Mt. Apo, $07^{\circ}00'\text{N}$, $125^{\circ}16'\text{E}$, 10 Nov. 2002, G. D. Alejandro 17 (PNH, Univ. Santo Tomas Hb.). **Mindoro Occidental:** San Nicolas, Magsaysay, $12^{\circ}21'\text{N}$, $121^{\circ}06'\text{E}$, 20 Sep. 2002, D. M. Madulid & J. C. Castro 13 (US), 15 (WAG), 16 (L, UBT).

8. *Mussaenda grandifolia* Elmer, Leaflet Philipp. Bot. 1: 12–13. 1906. TYPE: Philippines. Paragua: Pt. Separation, $09^{\circ}05'\text{N}$, $118^{\circ}07'\text{E}$, Feb. 1903, E. D. Merrill 817 (lectotype, designated by Jayaweera [1964: 115], US [barcode] 000435787!).

Shrubs 3–4 m tall; young twigs greenish brown, densely velvety, the trichomes less than 12-celled, white to brownish; older branches with few lenticels, grayish brown, glabrous or with few scattered trichomes. Leaf blades ovate or elliptic to obovate, $16\text{--}32 \times 7.5\text{--}15$ cm, membranaceous, sparsely velvety adaxially, densely velvety abaxially, especially on the midrib and veins, margins ciliate, apex acute, not conduplicate, base cuneate, or long attenuate; secondary veins in 11 to 14

pairs, prominulous above; petioles 1.5–3 cm, densely velvety; stipules triangular, $7 \times 3\text{--}4$ mm at the base, deciduous, abaxially with dense indument, adaxially with sparse indument; apex entire or bifid, $1/8$ of length, the stipule lobes not diverging; colleters numerous, in continuous rows at the base. Inflorescences spreading, densely velvety; bracts few, ovate, entire, $1.5\text{--}2 \times 0.5\text{--}1.5$ mm, densely velvety on both sides; pedicels 1.5–2 mm, with appressed trichomes. Flowers odorless; calyx tubes cup-shaped to shortly tubular, 4 mm long, densely velvety; calyx lobes lanceolate or subulate, not recurved, $0.8\text{--}2.5 \times 0.7\text{--}1$ mm, velvety on both sides, occasionally with a single calycophyll; colleters as 1 to 3 pairs per lobe, in sinuses between calyx lobes; calycophylls with blades broadly ovate, 5-nerved, $4.5\text{--}7 \times 4\text{--}4.5$ cm, yellowish white, sparsely pubescent along nerves on both surfaces, margins ciliate, apex acuminate, base attenuate; calycophyll stalks 1.5–2.5 cm, densely pubescent; corolla buds and open flowers densely velvety; corolla tubes infundibular, swollen portion around anthers indistinct, 2.5–2.9 cm long, yellowish white, without tuft of trichomes surrounding the opening, internally glabrous in long-styled flower morphs, short-styled flower morphs not seen; lobes ovate, $4 \times 3\text{--}4$ mm, yellow, abaxially velvety, adaxially papillate; apex not recurved, without filiform apical appendages; stamens inserted around the middle in long-styled flower morphs, filaments glabrous, anthers linear, 3.2–4.2 mm in long-styled flower morphs, glabrous, apex acute; pollen diameters to $14.85\text{ }\mu\text{m}$, apertures 4; ovary $4.5 \times 2\text{--}2.5$ mm, style 22 mm in long-styled flower morphs, stigma 10 mm, smooth, not recurved and included in long-styled flower morphs. Fruits ellipsoid, $1\text{--}1.3 \times 0.8\text{--}0.9$ cm, without warts and vertical ridges, green, calyces persistent, densely velvety; mesocarp 0.7–0.9 mm thick; fruiting pedicels 2–2.5 mm, densely velvety; seeds $0.64\text{--}0.77 \times 0.43\text{--}0.53$ mm; exotesta cells with 2 to 4 pores on the inner tangential walls, tuberculate thickenings absent.

Local names. Buyon-buyon (Pal); Malabuyon (Tag), according to Alejandro (pers. obs.).

Phenology. *Mussaenda grandifolia* has been collected in flower and fruit in February and March.

Distribution and habitat. *Mussaenda grandifolia* is endemic to Palawan, from Paragua Province. It has been collected in lower montane forest, on ultramafic slopes, and at altitudes from 40 to 550 m.s.m.

Discussion. Merrill mentioned only one collection, *Merrill 817*, in his 1906 protologue. As a Bureau of Science collection for the flora of the Philippines, one duplicate would have been deposited at PNH and

destroyed along with the herbarium in World War II. The surviving duplicate at US was identified as “Type” in Jayaweera’s treatment of Philippine *Mussaenda* (1964: 112) and specified as “US-lectotype” (1964: 115).

This species is the only Philippine representative with a velvety indumentum on the vegetative and reproductive parts and without unicellular trichomes inside the corolla tube. *Mussaenda grandifolia* appears to have a restricted and endemic distribution in Palawan. Its most recent collection was in 1984 at Mount Beaufort deposited at PNH.

Additional specimens examined. PHILIPPINES. **Palawan:** Mt. Beaufort, NNW spur, E side, $08^{\circ}46'N$, $117^{\circ}47'E$, *Ridsdale 35* (PNH); San Antonio Bay, $08^{\circ}39'N$, $117^{\circ}36'E$, *Merrill 865* (US).

9. *Mussaenda lanata* C. B. Rob., Philipp. J. Sci. 6(Pt. C): 357. 1911. TYPE: Philippines. Benguet: Luzon, Antimok, $16^{\circ}25'N$, $120^{\circ}35'E$, May 1909, *E. D. Merrill 6681* (lectotype, designated by Jayaweera [1964: 117], US [barcode] 000711179!). Figure 9.

Shrubs or trees, 2–5 m tall; young twigs green to grayish brown, densely hirsute, the trichomes more than 12-celled, white to brown; older branches with few to many lenticels, reddish or grayish brown, glabrous or with few scattered trichomes. Leaf blades ovate or obovate to orbicular, $10.5\text{--}30 \times 6.5\text{--}16.5$ cm, membranaceous to subcoriaceous, sparsely to densely pubescent above, densely pubescent, especially on midrib and veins underneath; margins ciliate; apex abruptly acute to acuminate, not conduplicate; base cuneate to obtuse; secondary veins in 8 to 13 pairs, prominulous above; petioles 1–8 cm long, densely hirsute. Stipules triangular or ovate, $8\text{--}18.5 \times 5\text{--}8.5$ mm at the base, deciduous, abaxially with dense indument, adaxially with dense indument only at the base and apex; apex entire or bifid $1/8$ of length, the lobes not diverging; colleters numerous, in continuous rows or in groups of 2 at the base. Inflorescences spreading, densely hirsute; bracts few, linear-lanceolate, entire, $3\text{--}7.5 \times 0.8\text{--}1.5$ mm, densely hirsute underneath, sparsely to densely hirsute above. Flowers odorless; pedicels 1.5–2 mm, with densely appressed trichomes; calyx tubes cup-shaped to shortly tubular, 3.5–4 mm long, densely pilose to hirsute; calyx lobes lanceolate or subulate, not recurved, $5.5\text{--}6.5 \times 1\text{--}1.2$ mm, apex acuminate, pilose or hirsute on both sides, occasionally with a single calycophyll; colleters as 1 pair per lobe, in sinuses between calyx lobes; calycophylls ovate to elliptic, 5-nerved, $4\text{--}5.5 \times 3\text{--}4$ cm, white, sparsely pubescent along nerves on both surfaces, margins ciliate, apex acute or acuminate, base cuneate; calycophyll stalks 1–1.7 cm, densely pilose;

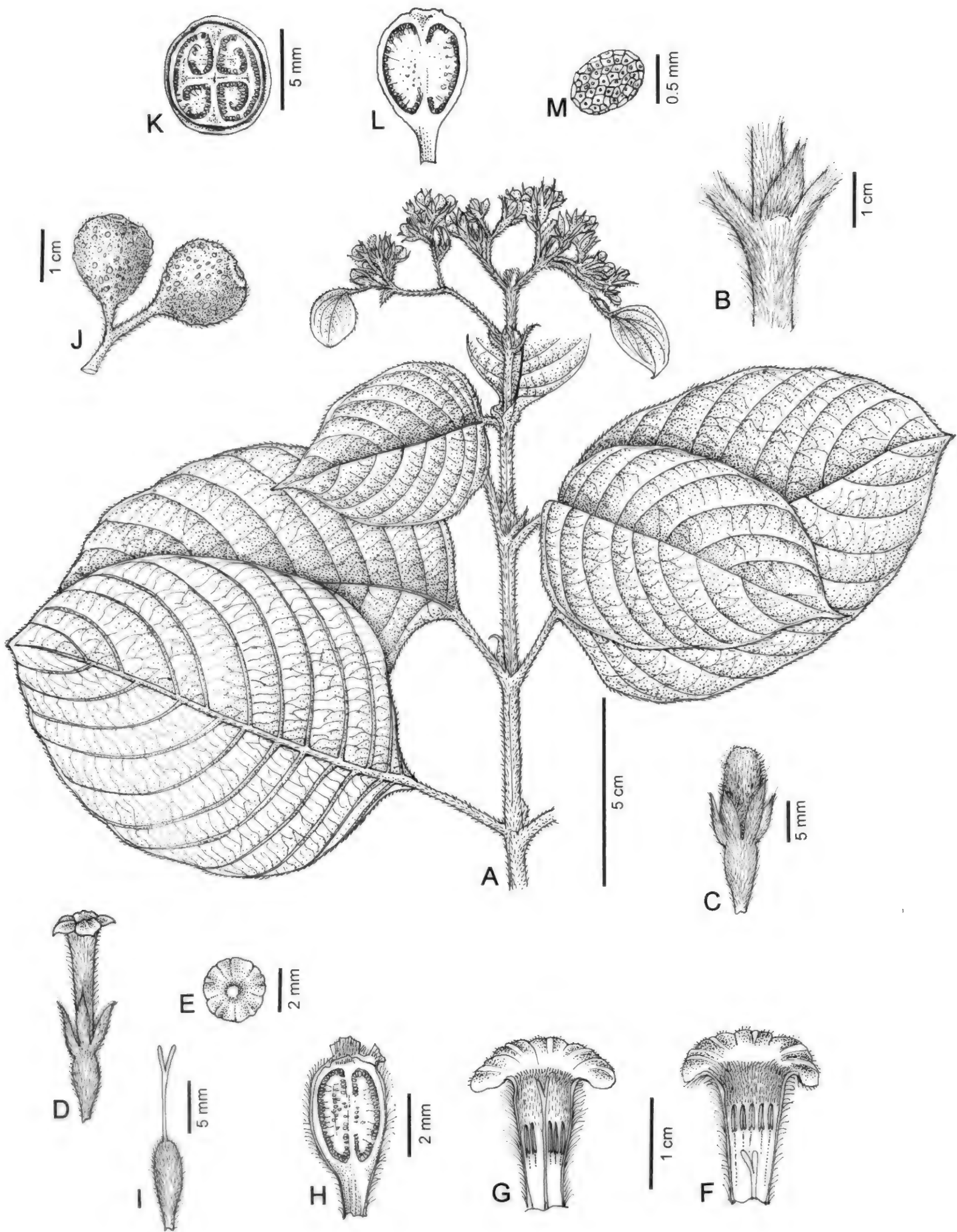


Figure 9. *Mussaenda lanata* C. B. Rob. —A. Flowering branch. —B. Portion of stem with stipule. —C. Flower bud. —D. Open anthesal flower. —E. Corolla lobes in top view. —F. Short-styled flower morph, corolla tube dissected open in longitudinal section. —G. Long-styled flower morph, corolla tube dissected open in longitudinal section. —H. Longitudinal section through ovary. —I. Calyx, style, and stigma of long-styled flower morph, with the corolla and calyx lobes removed. —J. Two fruits. —K, L. Fruit sections showing seed attachments on placentas, with cross and longitudinal sections, respectively. —M. Seed. A–C are taken from *Williams 1011* (NY); D–E, G–I, from *Santos 5678* (L); F, from *Mabesa 35292* (PNH); J–M, from *Alejandro 101* (UBT).

corolla buds densely pilose, remaining pilose all over or becoming pilose only on the upper half and with few scattered trichomes below in open flowers; corolla tubes infundibular, swollen portion around anthers indistinct, 1.1–1.5 cm long, yellowish white, without tuft of trichomes surrounding the opening; short-styled flower morphs with sparsely to densely long, unstriated, ribbon-like trichomes internally to the base of anthers or to the short filaments from the top; long-styled flower morphs with sparsely short, striated, ribbon-like trichomes internally to the base of anthers from the top; corolla lobes somewhat truncate and broader than long, 1.2–1.5 × 2.2–3 mm, yellow, abaxially pilose, adaxially papillate; apex not recurved, with or without 1-mm-long filiform apical appendages; stamens inserted to distal 1/4 in short-styled flower morphs, around middle in long-styled flower morphs, filaments glabrous, anthers linear or linear to narrowly lanceolate, 3.5–4.5 mm in short-styled flower morphs, 3–4 mm in long-styled flower morphs, glabrous, apex acute; pollen diameters to 15.75 µm, apertures 4; ovary 3.5–4.5 × 1.5–2 mm, style 1.6 mm in short-styled flower morphs, 5–7 mm in long-styled flower morphs, stigma 1.8 mm in short-styled flower morphs, 3–5 mm in long-styled flower morphs, smooth, not recurved and included in long-styled flower morphs. Fruits ovoid to ellipsoid, 1.2–1.7 × 0.6–0.8 cm, with dense warts, without vertical ridges green; calyces deciduous, glabrous or sparsely pubescent; mesocarp 0.4–0.6 mm thick; fruiting pedicels 2–4 mm, sparsely pubescent; seeds 0.43–0.56 × 0.36–0.43 mm; exotesta cells with 3 to 6 pores on the inner tangential walls, tuberculate thickenings slightly prominent or inconspicuous.

Local names. Bodos (Bon); Bodas (Igt), according to Alejandro (pers. obs.).

Phenology. *Mussaenda lanata* has been observed to flower from January to May and October to December. Fruiting occurs in May and October to December.

Distribution and habitat. *Mussaenda lanata* is restricted to the Luzon Region, where it is known from the provinces of Abra, Apayao, Benguet, Ilocos Sur, and Mountain. It has been collected from low- to mid-altitude secondary forests, on streamsides, on clay-loamy soils, and from altitudes ranging from 350 to 1200 m.s.m.

Discussion. Merrill mentioned only one collection, *Merrill 6681*, in his 1911 protologue. As a Bureau of Science collection for the flora of the Philippines, one duplicate would have been deposited at PNH and destroyed during World War II. The surviving duplicate at US was identified as “Type” in

Jayaweera’s treatment of Philippine *Mussaenda* (1964: 116) and “US-lectotype” (1964: 117). No other duplicates have been found.

Mussaenda lanata can be easily distinguished by its very short, infundibular corolla tubes to 1.5 mm, which are usually covered by the calyx lobes before anthesis. This species is also remarkable by its ovate to obovate or orbicular leaves, long stipules to 18.5 mm, and broader than long, truncate corolla lobes. Three *Mussaenda* species, *M. anisophylla*, *M. villosa* Wall., and *M. magallanensis*, were earlier suggested as close allies of *M. lanata* (Robinson, 1911; Jayaweera, 1964), probably by vegetative morphology and indumenta. However, it seems that *M. lanata* is more closely related to *M. chlorantha* and *M. vidalli* based on the inflorescence and flower morphology in that these three generally have densely pubescent inflorescences; few, long, and narrow bracts; short flower pedicels to 1.5–2 mm; and infundibular, pubescent corolla tubes. These three *Mussaenda* species differ in the shape of leaf blades, size of corolla tubes, and morphology of corolla lobes. Moreover, they are all found in Luzon, but *M. chlorantha* extends to Negros Oriental (Visayas), while *M. vidalli* is diverse in the provinces of Visayas and Mindanao.

Additional specimens examined. PHILIPPINES. **Abra:** 17°38’N, 120°52’E, *Ramos 7254* (NY). **Apayao:** Luzon Region/Island, Calanasan, Tanglagan, Mt. Duraragan, 18°14’N, 121°02’E, *Alejandro 101* (UBT, *Univ. Santo Tomas Hb.*). **Benguet:** Kapungun to Sagpat, 17°35’N, 120°23’E, *Clemens 17249* (NY), *Loher A. 1524* (US), *Merill 1768* (A, MO, NY); Sablan, 16°21’N, 120°40’E, *Elmer 6195* (NY), *Williams 1011* (A, NY), *1588* (NY); Baguio, Kennon, Camp 3, 16°24’N, 120°38’E, *Mabesa 35292* (PNH); Baguio, 16°29’N, 120°35’E, *Elmer 8976* (NY, US). **Ilocos Sur:** Tirad Pass, Sitio Sisim, Barrio Mabatano, Mt. Tirad Concepcion, 17°08’N, 120°38’E, *Santos 5678* (L); Lepanto, Cervantes trail, 16°59’N, 120°44’E, *Ramos & Edaño 38103* (A). **Mountain:** Bontoc, 17°05’N, 120°58’E, *Ramos & Edaño 38134* (A).

10. *Mussaenda liedea* Alejandro, sp. nov. TYPE: Philippines. Palawan: Palawan Island, Taytay, Ibangley, 10°49’N, 119°30’E, 20 Nov. 2002, *G. J. D. Alejandro 89* (holotype, UBT!; isotypes, NY [barcode] 00888328!, *Univ. Santo Tomas Hb.*!, US!). Figure 10.

Haec species ab aliis speciebus generis foliis ovatis usque ellipticis vel obovatis usque ad 28.5 × 10.5 cm utrinque sparsim hirsutis, venis secundariis adaxialiter prominulis, inflorescentiis multifloris late patentibus, tubo calycis longo et fructibus dense verrucosis distinguenda.

Shrubs 2–4 m tall; young twigs greenish brown, sparsely hirsute, the trichomes more than 12-celled, white to brownish; older branches lenticellate, grayish to reddish brown, glabrous or with few scattered trichomes. Leaf blades ovate to elliptic or sometimes obovate, 6.4–28.5 × 4.1–10.5 cm, membranaceous, sparsely hirsute

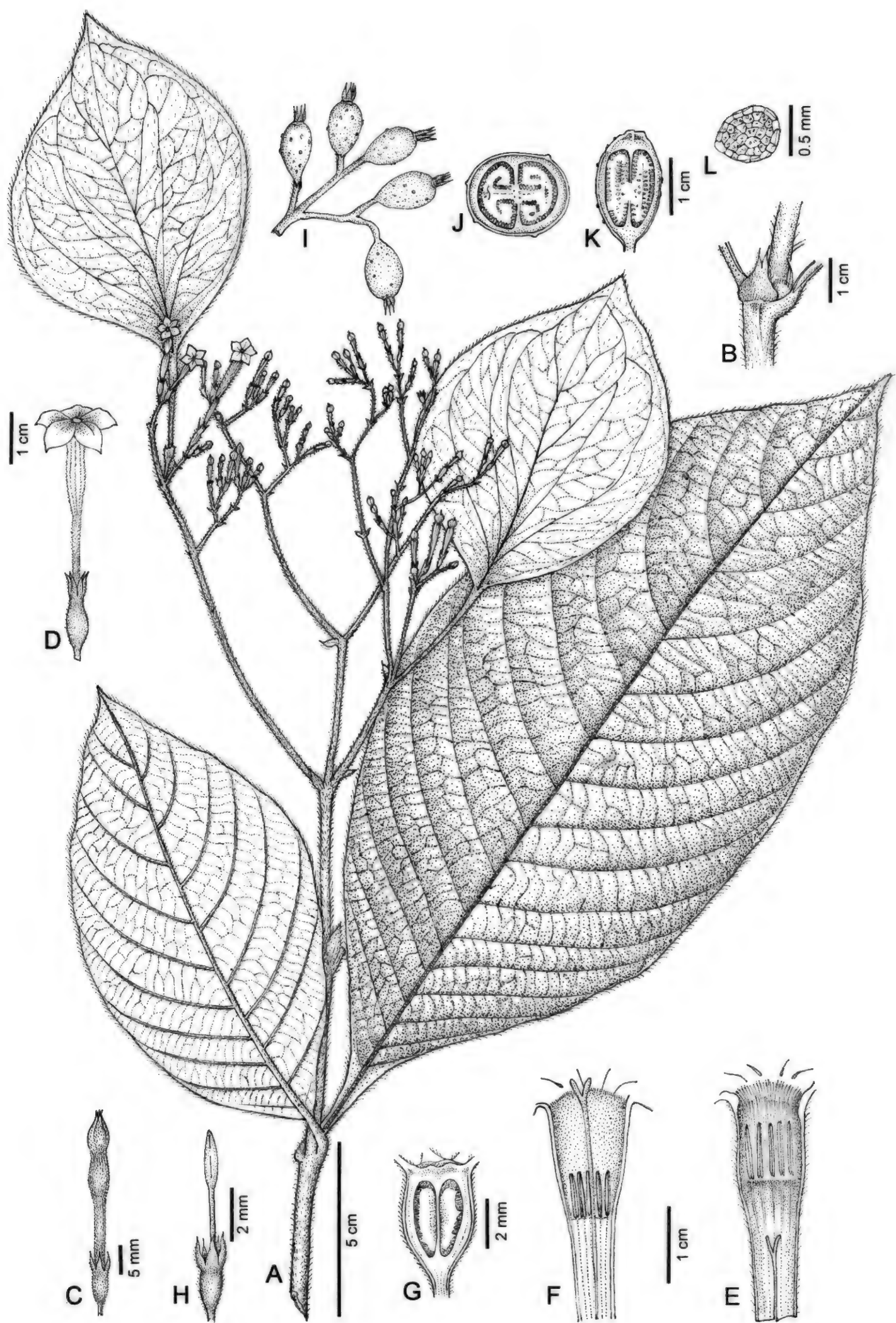


Figure 10. *Mussaenda liedeae* Alejandro. —A. Flowering branch. —B. Portion of stem with stipule. —C. Flower bud. —D. Open anthesis flower. —E. Short-styled flower morph, corolla tube dissected open in longitudinal section. —F. Long-styled flower morph, corolla tube dissected open in longitudinal section. —G. Longitudinal section through ovary. —H. Calyx, style, and stigma of short-styled flower morph, with the corolla removed. —I. Five fruits typically with dense warts. —J, K. Fruit sections showing seed attachments on placentas, in cross and longitudinal sections, respectively. —L. Seed. A–E, G–H are taken from the holotype *Alejandro 89* (UBT); F, I–L, from the paratype *Alejandro 88* (L).

on both sides, especially along midrib and veins, margins ciliate, apex acuminate to subcaudate, not conduplicate, base cuneate to long attenuate; secondary veins in 8 to 16 pairs, prominulous above; petioles 0.3–2 cm, hirsute; stipules triangular, $8.5\text{--}11.5 \times 3.5\text{--}7$ mm at the base, deciduous, abaxially hirsute, adaxially hirsute only at the base; apex bifid $1/4$ to \pm half of length, the lobes slightly diverging; colleters numerous, in continuous rows, or in groups of 2 at the base. Inflorescences widely spreading, sparsely hirsute to glabrate; bracts few, linear to narrowly lanceolate, entire or trilobed, $3.5\text{--}7 \times 1\text{--}2$ mm, pubescent underneath, glabrous above; flower pedicels 1–2 mm, with sparse appressed trichomes. Flowers crowded, odorless; flower buds densely pubescent; calyx tubes cup-shaped to tubular, 5–6 mm, pubescent; calyx lobes subulate, not recurved, $2\text{--}4 \times 1\text{--}1.5$ mm, pubescent outside, glabrous inside, occasionally with a single calycophyll; colleters as 1 to 3 pairs per lobe, in sinuses between calyx lobes; calycophylls ovate to orbicular, 5-nerved, $(4.5\text{--})9\text{--}10.5 \times (3.8\text{--})7\text{--}8.2$ cm, white or cream, glabrous or sparsely pubescent along nerves on both surfaces, margins ciliate or glabrous, apex acuminate, base cuneate to obtuse, calycophyll stalks 2–2.5 cm, pubescent; corolla buds densely pubescent, becoming pubescent only on upper half and with few scattered trichomes below in open flowers, corolla tubes cylindrical, forming a distinctly swollen part around anthers, 2.5–3 cm, cream or yellowish white, with or without tuft of trichomes surrounding the opening; short-styled flower morphs with dense, long, unstriate, ribbon-like trichomes internally to the base of anthers from the top; long-styled flower morphs with sparse globular, striate trichomes internally to base of anthers or to the short filaments from the top; corolla lobes ovate, $4\text{--}7 \times 3\text{--}4$ mm, golden-yellow or yellow-orange, abaxially sparsely pubescent, adaxially papillate, apex recurved, with 1–2 mm filiform apical appendages; stamens inserted to distal $1/4$ in short-styled flower morphs, inserted to the middle in long-styled flower morphs, filaments glabrous, anthers linear, 5–6 mm in short-styled flower morphs, 4.5–5.5 mm in long-styled flower morphs, glabrous, apex acute; pollen diameter to $10.8\text{ }\mu\text{m}$, apertures 4; ovary $4\text{--}5 \times 2\text{--}2.5$ mm; style 2–3 mm in short-styled flower morphs, 20–25 mm in long-styled flower morphs; stigma 1.5–2 mm in short-styled flower morphs, 6–9 mm in long-styled flower morphs, papillose, not recurved and semi-exserted in long-styled flower morphs. Fruits ovoid, $1.5\text{--}1.8 \times 1\text{--}1.1$ cm, with warts, without vertical ridges, green, calyces \pm persistent or deciduous, glabrous or puberulous; mesocarp 0.6–1 mm thick; fruiting pedicels 2–4 mm, glabrous or puberulous; seeds $0.58\text{--}0.9 \times 0.48\text{--}0.8$ mm; exotesta cells with 2 to 6 pores on the

inner tangential walls, tuberculate thickenings slightly prominent.

Local names. Buyan (Pal); Boyon (Tbw); Sigidago (Tbw), according to Alejandro (pers. obs.).

Etymology. The epithet of the new species honors Sigrid Liede-Schumann (1957–), who has done much to further the studies of the Apocynaceae–Asclepiadoideae, and who was an advisor who guided the first author in various aspects of taxonomy.

Phenology. *Mussaenda liedae* has been observed in flower in January, April, October to December, and in fruit November to December.

Distribution and habitat. *Mussaenda liedae* is endemic to Palawan, found in savanna forests, on slopes near the roadsides, in thickets, on clay or sandy soils, and at altitudes ranging from 30 to 150 m.s.m.

IUCN Red List category. *Mussaenda liedae* is assessed as Critically Endangered or CR, C2a(i), according to IUCN (2001) criteria. The population size is estimated to number fewer than 2500 mature individuals. A continuing decline in the number of mature individuals is projected, and no subpopulation is estimated to contain more than 250 mature individuals. The habitat of this species is threatened by human land use.

Discussion. This species was first collected in 1984 (*Ridsdale 1542*), and the only flowering specimen in L was initially labeled as *Mussaenda* cf. *setosa*. Similarities between *M. liedae* and *M. setosa* include the hirsute indumentum in young twigs and inflorescence axes, the larger size of leaf blades, to 28.5 cm and 29.8 cm, respectively, the shape and size of corolla lobes, ovate and to 7 mm and 6 mm, respectively, and the presence of globular trichomes inside corolla tubes of long-styled flower morphs. Recent collections of *M. liedae* at the same locality as *Ridsdale 1542*, near the Taytay municipality, showed its distinctness from *M. setosa*, which is also found in Palawan. *Mussaenda liedae* is characterized by ovate or obovate leaves that are only sparsely hirsute, flowers spreading with pedicels to 2 mm, and by longer calyx tubes to 6 mm with smaller lobes to 4 mm. In contrast, *M. setosa* has elliptic to ovate leaves of similar size that are setose, flowers congested with pedicels to 1 mm, and shorter calyx tubes to 3.5 mm with longer lobes to 6 mm.

Paratypes. PHILIPPINES. **Palawan:** Roxas, Sandoval, $10^{\circ}19'\text{N}$, $119^{\circ}21'\text{E}$, 18 Nov. 2002, G. J. D. Alejandro 88 (L); Taytay municipality, N of Embarcadero, area near Igang, $10^{\circ}50'\text{N}$, $119^{\circ}28'\text{E}$, 26 Apr. 1984, C. *Ridsdale 1542*

(L); Taytay, Ibangle, 10°49'N, 119°30'E, 20 Nov. 2002, G. J. D. Alejandro 90 (PNH, UBT, Univ. Santo Tomas Hb.).

11. *Mussaenda macrophylla* Wall. in Roxb, Fl. Ind. 2 [Carey & Wallich ed.]: 228. 1824, non *Mussaenda macrophylla* Schumacher & Vahl., Beskr. Guin. Pl.: 118. 1827, nom. illeg., nec *Mussaenda macrophylla* Kurz, Forest Fl. Burma 2: 57. 1877, nom. illeg. TYPE: Nepal. s. loc., 1821, Wallich Cat. no. 6255 (lectotype, designated here, K [barcode] K000031997 digital image!).

Shrubs or (sub)scandent shrubs 2–4 m tall; young twigs green to grayish brown, the trichomes grayish or brown. Leaf blades broadly ovate to elliptic or elliptic to lanceolate, 7–26 × 2.5–15 cm, membranaceous, pilose or puberulous above, sparsely pubescent or hirsute, especially on midrib and veins underneath, margins glabrous, apex acute to acuminate, not conduplicate, base cuneate; secondary veins in 7 to 13 pairs, prominent above; petioles 0.5–4.2 cm, glabrous, villous or hirsute; stipules ovate or triangular, 5–13.5 × 3.5–9 mm at the base, deciduous, pubescent outside, glabrous or pubescent inside; apex bifid 1/4 to 3/4 of length, the stipule lobes diverging or not; colleters in continuous rows or in groups of 2 at the base. Inflorescences spreading or congested, pubescent or densely hirsute; bracts few, lanceolate or ovate, entire or trilobed, pubescent on both sides; flower pedicels 0.5–1.5 mm, with densely appressed trichomes. Flowers odorless; calyx tubes cup-shaped to shortly tubular, 3–5 mm, densely hirsute; calyx lobes oblong to lanceolate, not recurved, 3.2–14 × 1.2–4 mm, pubescent outside, glabrous or hirsute inside, occasionally with a single calycophyll or all lobes developed as calycophylls; colleters as 1 to 5 pairs per lobe, in sinuses between calyx lobes; calycophylls ovate or elliptic to lanceolate, 5-nerved, 2–9 × 0.5–7 cm, white, glabrous or puberulous along nerves on both surfaces, margins glabrous, apex acute or acuminate, base cuneate or attenuate; calycophyll stalks 0–2.5 cm, puberulous, setose or hirsute; corolla buds densely hirsute, remaining hirsute all over or only on the upper half and with few scattered trichomes below in open flowers; corolla tubes cylindrical, forming a distinctly swollen part around anthers, 2–3.2 cm, with or without tuft of trichomes surrounding the opening; short-styled flower morphs with long, unstriated, ribbon-like trichomes internally to the base of anthers from the top; long-styled flower morphs with sparse striate, ribbon-like trichomes internally to short filaments from the top; corolla lobes elliptic to broadly ovate or orbicular 3.5–5 × 4–6.5 mm, yellow, abaxially pubescent or sparsely hirsute, adaxially

papillate, apex not recurved, with or without filiform apical appendages; stamens inserted to distal 1/4 in short-styled flower morphs, around middle in long-styled flower morphs, filaments glabrous; anthers linear, 5–5.7 mm in short-styled flower morphs, 5 mm in long-styled flower morphs, glabrous, apex acute; ovary 3.5–5.5 × 2–2.5 mm, style 3.5–14 mm in short-styled flower morphs, 16–23 mm in long-styled flower morphs, stigma 2.5–4 mm in short-styled flower morphs, 2.5–7.5 mm in long-styled flower morphs, smooth, not recurved and included in long-styled flower morphs. Fruits oblong-ovoid, 1–1.2 cm, with sparse to dense warts, without vertical ridges, green or dark purple; calyces deciduous, sparsely pubescent; seeds 0.67–1.03 × 0.48–0.73 mm, exotesta cells with 2 to 6 pores on the inner tangential walls, tuberculate thickenings slightly prominent.

Discussion. In the protologue of his new species, Wallich designated no type specimen but mentioned two Nepalese localities, “mountains of Chundra-giria and Nagarjoun,” showing that his description (Roxburgh, 1824: 228) is based on at least two different gatherings. In Wallich’s Catalogue (Wallich 1832 [1828–1849]) only a single entry for *Mussaenda macrophylla* is found under the number 6255, including the data “Napalea 1821.” All Wallich specimens that have been traced bear this number and are regarded as syntypes. One specimen, K000031997, bears the number 6295, additionally added in pencil by a different hand. However, the number 6295 in Wallich’s Catalogue referred to another species (*Hopea wightiana* Wall.), so that this addition was obviously a typographic error. The Kew sheet (barcode, K000031997) is regarded as belonging to the original set of Wallich specimens and is here chosen to serve as lectotype. All other syntypes may belong to different gatherings, and it seems advisable to restrict the type to a single lectotype.

Additional specimens examined. INDIA. Nepal (s. loc.), 1821 (syntypes, GH [bc] 00096260 digital image!, E [bc] 00438211 digital image!, E [bc] 00438212 digital image!, K [bc] K001123448 digital image!, K [bc] K001123449 digital image, NY [bc] 00132295!).

KEY TO THE VARIETIES OF *MUSSAENDA MACROPHYLLA*

- 1a. Shrubs or scandent shrubs; leaf blades puberulous adaxially, petioles more than 1 cm long; calyx lobes occasionally with a single calycophyll.
 - 2a. Stipules 7–12 mm long; calyx lobes 3.2–8 × 2–2.5 mm; corolla 2.3–2.6 mm long, without tuft of trichomes in the opening; plants from the Philippines . . . 11a. *M. macrophylla* Wall.
var. *brevipilosa* Jayaw.
 - 2b. Stipules 12–13.5 mm long; calyx lobes 8.5–14 × 1.2–4 mm; corolla 2.4–3.2 mm long,

with tuft of trichomes in the opening; plants from southern Asia (excluding the Philippines) 11c. *M. macrophylla* Wall. var. *macrophylla*

- 1b. Erect shrubs; leaf blades pilose adaxially, petioles 1 cm or less; calyx lobes all developed into calycophylls; plants from India
..... 11b. *M. macrophylla* Wall. var. *grandisepala* (Jayaw.) Alejandro

11a. *Mussaenda macrophylla* Wall. var. *brevipilosa* Jayaw., J. Arnold Arbor. 45: 117. 1964. TYPE: Philippines. Batanes: Batanes Island, May–June 1907, *E. Fenix* 3770 (holotype, NY [barcode] 00689069!; isotype, US!). Figure 11.

Shrubs or scandent shrubs 3–4 m tall; young twigs sparsely hirsute, the trichomes more than 12-celled, brown; older branches with few to many lenticels, reddish brown, glabrous. Leaf blades $10\text{--}26 \times 5\text{--}15$ cm, puberulous above, sparsely pubescent underneath; secondary veins in 8 to 13 pairs; petioles 0.6–4.2 cm long, glabrous or sparsely hirsute; stipules triangular, $7\text{--}12 \times 3.5\text{--}7$ mm at the base, with sparse indument on both sides; apex bifid, the stipule lobes not diverging; colleters numerous. Inflorescences densely hirsute; bracts $5\text{--}7 \times 1\text{--}2.5$ mm, sparsely pubescent underneath, glabrous or puberulous above; flower pedicels 1–1.5 mm. Flowers with calyx tubes 3–3.5 mm; calyx lobes $3.2\text{--}8 \times 2\text{--}2.5$ mm, hirsute on both surfaces, occasionally with a single calycophyll; calycophylls ovate, $6.5\text{--}9 \times 3.3\text{--}7$ cm, base cuneate; calycophyll stalks 1.7–2.5 cm, puberulous; corolla tubes 2.3–2.6 cm long, without tuft of trichomes surrounding the opening; long-styled flower morphs with sparsely short trichomes inside; corolla lobes ovate to elliptic, $5 \times 4\text{--}5$ mm, without filiform apical appendages, abaxially sparsely hirsute; anthers 5–5.5 mm in short-styled flower morphs, 5 mm in long-styled flower morphs; pollen diameters to 15.3 μm , apertures 4; ovary 4–5.5 mm, style 3.5–4 mm in short-styled flower morphs, 18–19 mm in long-styled flower morphs, stigma 2.5–3 mm in short-styled flower morphs, 7–7.5 mm in long-styled flower morphs. Fruits globose to ellipsoid, green; mesocarp 0.3–0.5 mm thick; fruiting pedicels 3–4 mm; seeds $0.67\text{--}0.87 \times 0.48\text{--}0.72$ mm.

Local name. Kamaligi (Ivt), according to Alejandro (pers. obs.).

Phenology. This variety has been observed to flower from May to June, but the time of fruiting is not known.

Distribution and habitat. *Mussaenda macrophylla* var. *brevipilosa* is found in the Philippines, on

Batanes and Calayan Islands, from the provinces of Batanes and Cagayan, respectively, as well as from Rizal Province. The variety has been collected from low-altitude forests, on edges of forests, on riversides, on clay or sandy soils, and from altitudes ranging from 150 to 300 m.s.m.

Discussion. *Mussaenda macrophylla* var. *brevipilosa* differs from *M. macrophylla* var. *macrophylla*, the autonymic variety found in India, Myanmar, and China, by its smaller stipules, corolla, and calyx lobes. In addition, *M. macrophylla* var. *brevipilosa* has short, straplike trichomes inside the corolla of long-styled flower morphs, whereas in *M. macrophylla* var. *macrophylla* the corolla trichomes are longer in long-styled flower morphs.

Additional specimens examined. PHILIPPINES. **Batanes:** Batan Island, Mt. Iraya, $20^{\circ}22'\text{N}$, $121^{\circ}55'\text{E}$, *Quisumbing et al.* 79364 (PNH), 79931 (PNH); Mt. Matarem, $20^{\circ}27'\text{N}$, $121^{\circ}59'\text{E}$, *del Rosario* 79959 (PNH). **Cagayan:** Calayan Island, San Vicente, $19^{\circ}21'\text{N}$, $121^{\circ}24'\text{E}$, *Quisumbing & del Rosario* 79842 (PNH), 79858 (PNH); Mt. Babatngin, *Edaño* 79448 (A). **Rizal:** Mt. Lumutan, $13^{\circ}97'\text{N}$, $121^{\circ}97'\text{E}$, *Ramos & Edaño* 29719 (A).

11b. *Mussaenda macrophylla* Wall. var. *grandisepala* (Jayaw.) Alejandro, stat. nov. Basionym: *Mussaenda macrophylla* f. *grandisepala* Jayaw., J. Arnold Arbor. 44: 246. 1963. *Mussaenda pentasemia* C. E. C. Fisch., Bull. Misc. Inform. Kew 1928(7): 275. 1928. TYPE: India. Assam: Nhatial, Lushai Hills, July 1927, *N. E. Parry* 275 (lectotype, designated here, K [barcode] K000031998 [sheet V, ft.] digital image!; isotype, K [bc] K000031999 [IV, veg.] digital image!, K [bc] K000032000 [III, ft.] digital image!, K [bc] K000032001 [II, fr.] digital image!, K [bc] K000032002 [I, ft.], digital image!).

Shrubs 2–3 m tall; young twigs densely villous. Leaf blades $7\text{--}12 \times 2.5\text{--}6$ cm, sparsely pilose on both sides; secondary veins in 7 to 9 pairs; petioles 0.5–1 cm, densely villous; stipules broadly ovate, $5\text{--}10 \times 5$ mm at the base, with indument on both sides, apex bifid, the stipule lobes not diverging, colleters numerous. Inflorescences pubescent; bracts densely pubescent on both sides. Flowers subsessile; calyx tubes 3.5–4.5 mm; calyx lobes all developing into calycophylls; calycophylls oblong or elliptic to lanceolate, $2\text{--}7 \times 0.5\text{--}4$ cm, base attenuate; calycophyll stalks 0–2.5 cm, setose; corolla tubes 2 cm, with tuft of trichomes surrounding the opening; long-styled flower morphs with sparse short trichomes inside; corolla lobes orbicular to ovate, 3.5×4.5 mm, with filiform

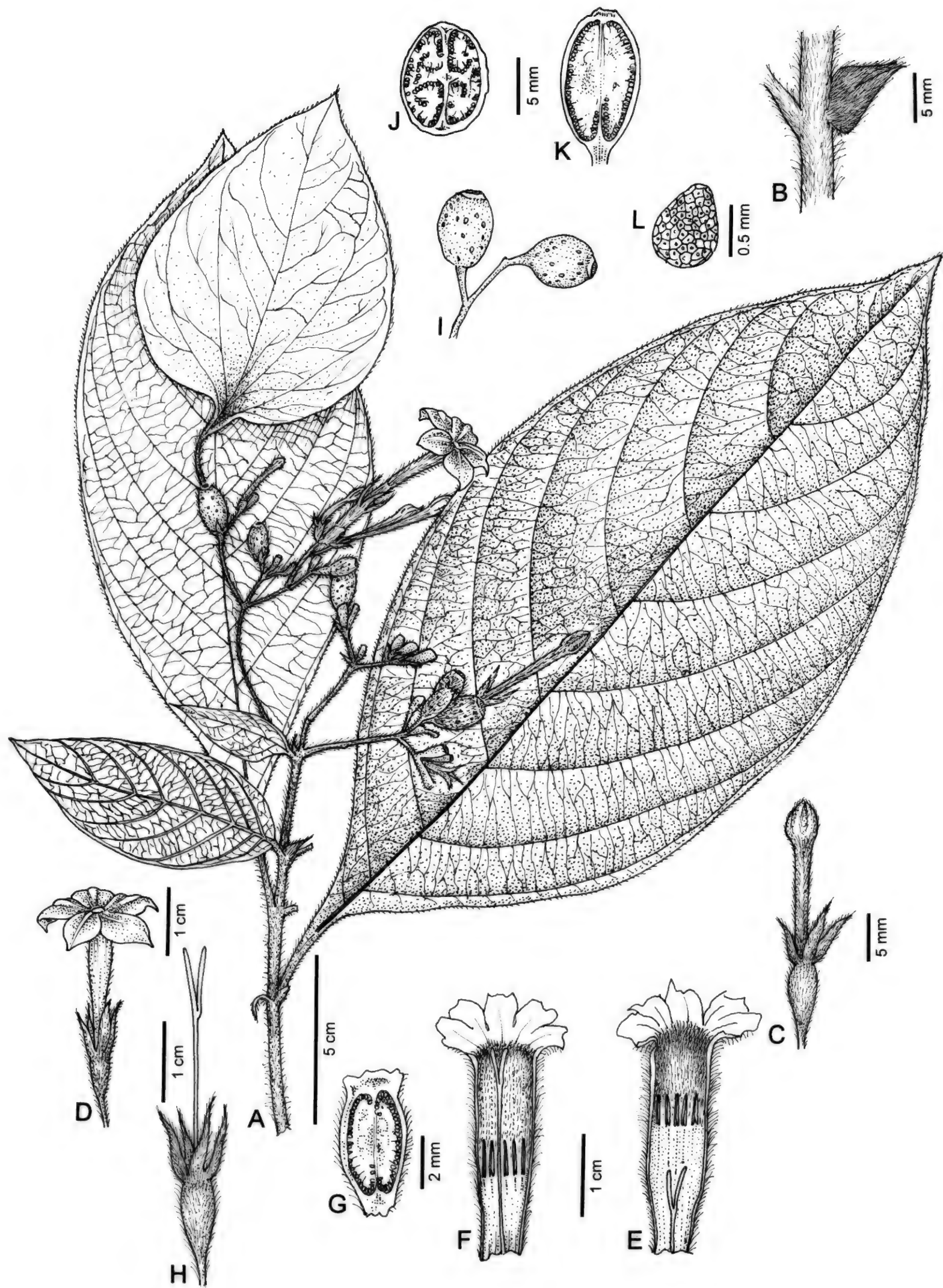


Figure 11. *Mussaenda macrophylla* Wall. var. *brevipilosa* Jayaw. —A. Flowering branch. —B. Portion of stem with stipule. —C. Flower bud. —D. Open anthesal flower. —E. Short-styled flower morph, corolla tube dissected open in longitudinal section. —F. Long-styled flower morph, corolla tube dissected open in longitudinal section. —G. Longitudinal section through ovary. —H. Calyx, style, and stigma of long-styled flower morph, with the corolla removed. —I. Two fruits. —J, K. Fruit sections showing seed attachments on placentas, in cross and longitudinal sections, respectively. —L. Seed. A, B, F, and H are taken from *Quisumbing & del Rosario* 79858 (PNH); E, from *Quisumbing & del Rosario* 79842 (PNH); C, D, I, and L, from the holotype *Fenix* 3770 (NY).

apical appendages, abaxially pubescent; anthers 5.2 mm in short-styled flower morphs, 5 mm in long-styled flower morphs; ovary 4–5 mm. Fruits not seen.

Phenology. *Mussaenda macrophylla* var. *grandisepala* has been collected in flower in July. Fruits were collected in July as noted from the type.

Distribution. *Mussaenda macrophylla* var. *grandisepala* is distributed in Assam, India, and is known from an altitude of 925 m.s.m. The variety does not occur in the Philippines.

Discussion. The name *Mussaenda pentasemia* is homotypic to *M. macrophylla* f. *grandisepala*. Fischer's 1928 protologue was published prior to Jayaweera's 1963 description of the form *grandisepala*. Fischer noted one collection "India. Assam, in the Lushai Hills at Nhatial, 925 m, Mrs. N. E. Parry 275..." The word "typus" or "type" was not used, but this was not required until 1958 (Art. 40.1, McNeill et al., 2012). Fischer's name at species rank has no priority over Jayaweera's epithet at infraspecific rank (Art. 11.2).

Five sheets of Parry 275 that were numbered sequentially (I, II, III, IV, V) were found at Kew, and there is no distinction of type among the sheets. Labels identifying "Type specimen" are found on sheets I and V, with "for fruits and seeds" further annotated on sheet I. A lectotype is designated among these five duplicates, from sheet V, which has abundant fertile material.

11c. *Mussaenda macrophylla* Wall. var. *macrophylla*.

(Sub)scandent shrubs; young twigs densely pubescent, the trichomes grayish brown, becoming brown when dry. Leaf blades 8–20 × 3–10.5 cm, puberulous above, hirsute underneath; secondary veins in 9 to 11 pairs; petioles 1–4 cm, densely hirsute; stipules ovate, 12–13.5 × 6–9.5 mm at the base, densely pubescent outside, glabrous or hairy inside; apex bifid, the stipule lobes diverging; colleters few to numerous. Inflorescences pubescent; bracts pubescent on both surfaces; fertile pedicels 0.5–1 mm; calyx tubes 3.5–5 mm; calyx lobes 8.5–14 × 1.2–4 mm, pubescent outside, glabrous to puberulous inside, occasionally with a single calycophyll; calycophylls ovate or broadly lanceolate, 6–9 × 2.5–6.7 cm, base cuneate; calycophyll stalks 1.7–2.5 cm, hirsute; corolla tubes 2.4–3.2 cm long, with tuft of trichomes surrounding the opening; long-styled flower morphs with sparse but long trichomes inside; lobes broadly ovate or

orbicular, 4–5 × 4–6.5 mm, with filiform apical appendages, abaxially pubescent; anthers 5–5.7 mm; ovary 3.5–4.5 mm, style 9–14 mm long in short-styled flower morphs, 16.5–23 mm in long-styled flower morphs, stigma 3.5–4 mm in short-styled flower morphs, 2.5–3.5 mm in long-styled flower morphs. Fruits oblong ovoid, dark purple; fruiting pedicels 3–4 mm; seeds 0.9–1.03 × 0.73 mm.

Phenology. This variety has been collected in flower from May to August and October, and in fruit in June, November to December and January.

Distribution and habitat. *Mussaenda macrophylla* var. *macrophylla* is known from India, Myanmar, and China and is found in low- to mid-altitude forests, ranging from 300 to 1500 m.s.m.

Additional specimens examined. CHINA. **Taiwan:** Botel Tobago, C. E. Chang 2754 (L). INDIA. Middle Andamans, Nimbutala, near Rangat, N. Bhargava 1757 (L).

12. *Mussaenda magallanensis* Elmer, Leaf. Philipp. Bot. 3: 996–997. 1911. TYPE: Philippines. Romblon: Sibuyan Island, Magallanes, Mt. Giting-giting [Mt. Guiting-guiting], 12°23'N, 122°35'E, May 1910, A. D. E. Elmer 12451 (lectotype, designated by Jayaweera [1964: 121], A [barcode] 00096196!; isolectotypes, E [bc] 00502304 digital image!, GH [bc] 00303908 digital image!, K [bc] 000740915 digital image!, L [bc] L000000795!, MICH [bc] 1108211 digital image!, MO [bc] 000716936 digital image!, NY [bc] 00132311!, U [bc] 0227258 digital image!, US [bc] 000137855!). Figure 12.

Shrubs 1.5–3 m tall; young twigs green to yellowish brown, hirsute, the trichomes more than 12-celled, brown; older branches with numerous lenticels, reddish brown, glabrous or with few scattered hairs. Leaf blades ovate to elliptic or orbicular to ovate, 6.5–28.5 × 3.5–15 cm, membranaceous, hirsute above, densely hirsute especially on midrib and veins underneath, margins ciliate, apex abruptly acuminate to subcaudate, not conduplicate, base cuneate; secondary veins in 10 to 13 pairs, prominulous above; petioles 0.6–5 cm, densely hirsute; stipules triangular to ovate, 7–16 × 3–9 mm at the base, deciduous, with dense indument on both sides; apex entire or bifid 1/4 of length, the stipule lobes not diverging; colleters numerous, in groups of 2 at the base. Inflorescences spreading or congested, densely hirsute; bracts few, linear to narrowly lanceolate, entire to trilobed, 4–11 × 1–2.5 mm, densely hirsute underneath,

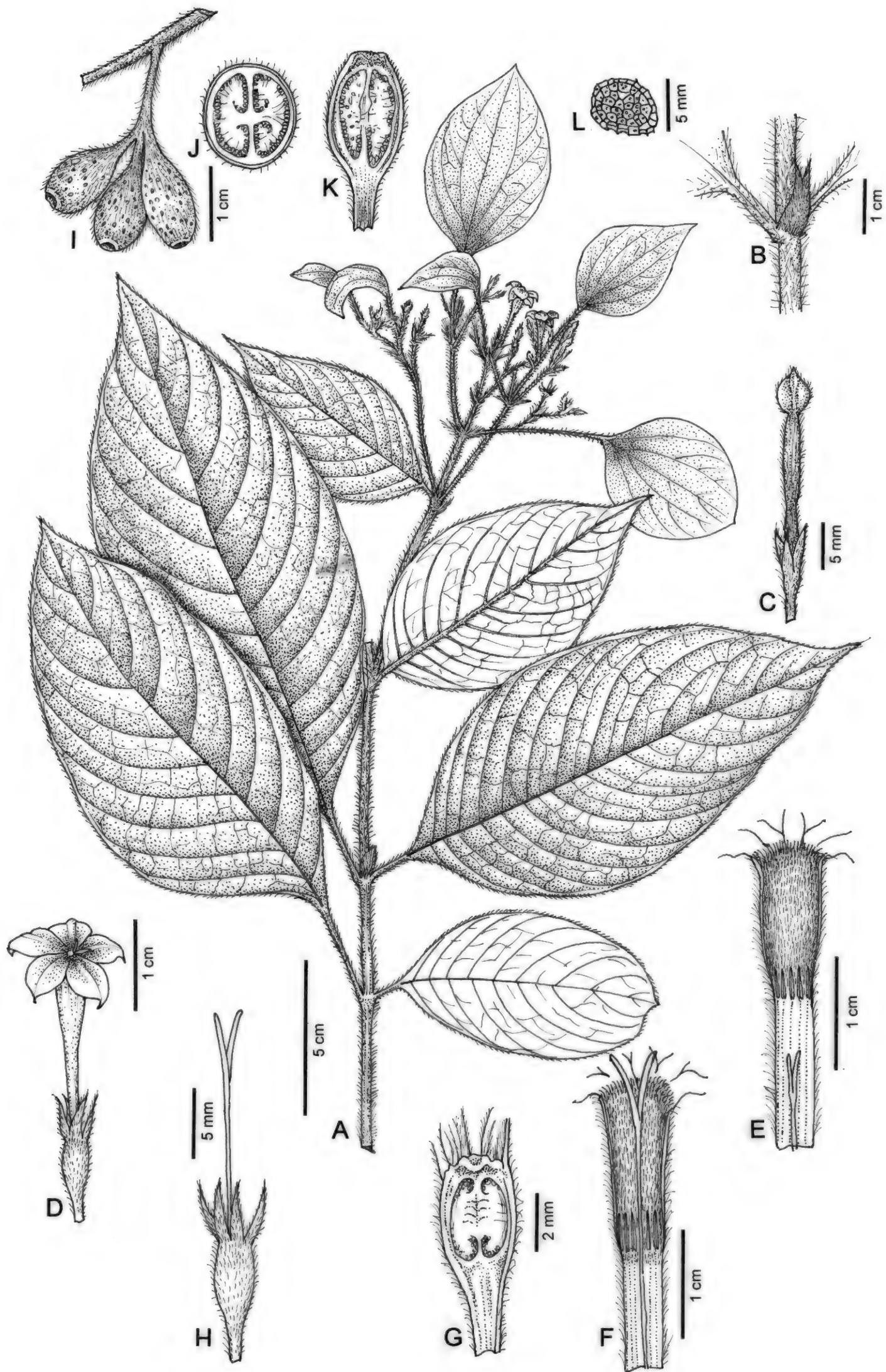


Figure 12. *Mussaenda magallanensis* Elmer. —A. Flowering branch. —B. Portion of stem with stipule. —C. Flower bud. —D. Open anthesal flower. —E. Short-styled flower morph, corolla tube dissected open in longitudinal section. —F. Long-styled flower morph, corolla tube dissected open in longitudinal section. —G. Longitudinal section through ovary. —H. Calyx, style, and stigma of long-styled flower morph, with the corolla removed. —I. Three fruits. —J, K. Fruit sections showing seed attachments on placentas, in cross and longitudinal sections, respectively. —L. Seed. A–E are taken from *Alejandro 5* (NY); F–L, from *Alejandro 3* (UBT).

glabrous or sparsely hirsute above; flower pedicels 2–2.5 mm, with appressed trichomes. Flowers odorless; calyx tubes cup-shaped to shortly tubular, 3–4 mm, hirsute; calyx lobes subulate, not recurved, $4\text{--}5 \times 0.5\text{--}1$ mm, hirsute on both surfaces, occasionally with a single calycophyll; colleters as 2 or 3 pairs per lobe, in sinuses between calyx lobes; calycophylls orbicular to elliptic or ovate, 5-nerved, $4\text{--}6 \times 4\text{--}5.5$ cm, white, glabrous above, pubescent only along nerves beneath, margins ciliate, apex acute or acuminate, base cuneate; calycophyll stalks 2–2.7 cm, pubescent; corolla buds pubescent, remaining either pubescent or usually glabrate in open flowers; corolla tubes cylindrical, forming a distinctly swollen part around anthers, 2–2.4 cm, yellowish white, with tuft of trichomes surrounding the opening; short-styled flower morphs with dense, long, unstriated, ribbon-like trichomes internally to base of anthers from the top; long-styled flower morphs with sparse short, striate, ribbon-like trichomes internally to short filaments from the top; corolla lobes ovate, $5\text{--}6 \times 3.5\text{--}5$ mm, orange to yellow, abaxially pubescent, adaxially papillate; apex not recurved, without filiform apical appendages; stamens inserted to distal 1/4 in short-styled flower morphs, around middle in long-styled flower morphs, filaments glabrous; anthers linear, 4–5 mm in short-styled flower morphs, 3–4 mm in long-styled flower morphs, glabrous, apex acute; pollen diameters to 16.2 μm , apertures 4, rarely 3; ovary $3\text{--}3.5 \times 2$ mm, style 4–5 mm in short-styled flower morphs, 12–14 mm in long-styled flower morphs, stigma 1–1.5 mm in short-styled flower morphs, 10–12 mm in long-styled flower morphs, smooth, recurved and semi-exserted in long-styled flower morphs. Fruits globose or obovoid, $1\text{--}1.3 \times 0.9\text{--}1.1$ cm, with sparse to dense warts, without vertical ridges, green, calyces deciduous, sparsely hirsute; mesocarp 0.8–1 mm thick; fruiting pedicels 4–7 mm, sparsely hirsute; seeds $0.5\text{--}0.67 \times 0.33\text{--}0.53$ mm, exotesta cells with 4 to 10 pores on the inner tangential walls, tuberculate thickenings slightly prominent.

Local names. Agboy (BisPn); Banay-dagat (Myn); Mabiun-tama, Mabiun-tina (Bng); Potenjsolab (unknown dialect), according to Alejandro (pers. obs.).

Phenology. *Mussaenda magallanensis* has been observed to flower from January to June, August, and October to December, with fruiting noted from September to November.

Distribution and habitat. *Mussaenda magallanensis* is known from the provinces of Mindoro,

Laguna, and Pampanga in the Luzon Region, from the provinces of Romblon (western Visayas) and Leyte (eastern Visayas), and from the province of Isabella on Basilan Island to the south. It has been collected from low- and mid-altitude forests, on mountainsides, on riversides, on brushlands, on clay-loamy or sandy soils, and at altitudes of 10–500 m.s.m.

Discussion. Elmer (1911a: 997) cited his “Type specimen number” as 12451, and Jayaweera (1964: 121) would later specify “A–lectotype; GH, NY, US–isotypes.” Additional isolectotypes (E, K, L, MICH, MO, and U) have been found, although Elmer’s type at PNH was destroyed during World War II.

Mussaenda magallanensis is similar to *M. anisophylla* in the hirsute indumentum of vegetative parts and inflorescences, in the generally ovate to elliptic shape of the leaves, in the size of the stipules (to 16 mm in *M. magallanensis*, to 15 mm in *M. anisophylla*), in the breadth and shape of the calycophylls (to 5.5 cm wide, orbicular to elliptic or ovate vs. to 6 cm wide, elliptic to ovate in *M. anisophylla*), and in the shape and length of the corolla lobes (ovate, to 6 cm long vs. broadly ovate, to 6 cm long in *M. anisophylla*). However, *M. magallanensis* differs from *M. anisophylla* by its dense pubescence in the corolla (vs. typically hirsute in *M. anisophylla*), by fewer bracts and shorter calyx lobes to 6 mm that are hirsute on both sides (vs. to 15 mm and hirsute externally in *M. anisophylla*), by the presence of trichomes at the mouth of the corolla, by the longer stigmata to 14 mm that are recurved and semi-exserted in long-styled flower morphs (vs. to 9 mm in *M. anisophylla*), by the smaller fruits to 1.3×1.1 cm (vs. to 2×1.2 cm in *M. anisophylla*), and by more pores (four to 10) on the inner tangential walls of the seed exotesta (two to six in *M. anisophylla*).

Additional specimens examined. PHILIPPINES. **Capiz:** Panay Island, $11^{\circ}17'N$, $122^{\circ}18'E$, *Edaño 46114* (NY); Antique Prov., locality not indicated, *McGregor 32499* (A). **Isabela:** San Mariano, $16^{\circ}59'N$, $122^{\circ}00'E$, *Ramos & Edaño 46977* (NY). **Laguna:** Luzon, Mt. Banahaw, $14^{\circ}04'N$, $121^{\circ}29'E$, *Ocampo 27899* (US); Majayjay, $14^{\circ}09'N$, $121^{\circ}08'E$, *Rivera & Duyag 75002* (BR); Balayhangin, Calawang, $13^{\circ}55'N$, $120^{\circ}52'E$, *Sulit 18877* (PNH); Los Baños, Inst. Pl. Breeding (IPB), $14^{\circ}10'N$, $121^{\circ}11'E$, *Alejandro 5* (BR, NY), Forestry Nursery, *Sulit 3442* (PNH). **Leyte:** Leyte Island, *Wenzel 442* (A, MO, US). **Mindoro Oriental:** Mindoro Island, Calapan, $13^{\circ}24'N$, $121^{\circ}10'E$, *Merrill 985* (NY), *986* (A, MO, NY); Pinamalayan, $13^{\circ}02'N$, $121^{\circ}29'E$, *Maliwanag 113* (PNH), *Ramos 40955* (US); N slope of Mt. Alinyaban, 5 km SW of Puerto Galera, $13^{\circ}28'N$, $120^{\circ}55'E$, *Burley 147* (L); Baco River, $13^{\circ}20'N$, $121^{\circ}05'E$, *McGregor 131* (NY, US), *Merrill 4072* (NY, US);

Sablayan, Ligaya, 12°50'N, 120°47'E, *Reed 40896* (PNH), 40902 (PNH); Puerto Galera, 13°28'N, 120°55'E, *Britton 120* (PNH), *Ramos 46385* (NY), *Santos 5212* (L). **Pampanga:** Clark, Fontana, 15°09'N, 120°32'E, *Alejandro 3* (L, UBT, *Univ. Santo Tomas Hb.*, WAG).

13. *Mussaenda milleri* Elmer ex Alejandro, sp. nov.
Mussaenda milleri Elmer, Leaflet. Philipp. Bot. 10: 3780. 1939, nom. inval. TYPE: Philippines. Nueva Ecija: Luzon, Mt. Umingan, Aug.–Sep. 1916, *Bureau of Sci. No. 26468* [*M. Ramos with G. Edaño*] (holotype, NY [barcode] 00132312!; isotype, US [bc] 001375472!).

Haec species ab aliis speciebus generis partibus vegetativis et inflorescentiis trichomatibus rubrobrunneis hirsutis, foliis parvis, venis lateralibus paucis (5 ad 11 paribus) et lobis corollae rubeoaurantiacis adaxialiter papillatis abaxialiter hirsutis differt.

Shrubs 3 m tall or more; young twigs green, sparsely to densely hirsute, the trichomes more than 12-celled, reddish brown; older branches with few lenticels, grayish brown, glabrous. Leaf blades elliptic to ovate, 7–12 × 3–6 cm, membranaceous, sparsely hirsute on both sides, especially on midrib and veins underneath, margins ciliate, apex acute to acuminate or subcaudate, recurved, not conduplicate, base obtuse to cuneate; midribs slightly sunken above; secondary veins in 5 to 11 pairs, prominulous above; petioles 1–2 cm, densely hirsute; stipules triangular to broadly lanceolate, 7–12 × 4–6 mm at the base, deciduous, with dense indument on both sides; apex bifid ± half of length, the stipule lobes not diverging; colleters numerous, in groups of 2 at the base. Inflorescences spreading, densely hirsute; bracts few, linear to narrowly lanceolate, entire, 2.5–4 × 1–1.5 mm, densely hirsute on both sides; flower pedicels with sparsely to densely appressed trichomes. Flowers odorless; calyx lobes not recurved, 3–5 mm, hirsute on both surfaces, occasionally with a single calycophyll; calycophylls elliptic, 5-nerved, 7.2 × 3.5 cm, yellowish white, sparsely pubescent along nerves of both surfaces, margins ciliate, apex acute to acuminate, base attenuate; calycophyll stalks 2.3 cm, densely pubescent; corolla buds hirsute, becoming hirsute only in upper half and with few scattered trichomes below in open flowers; corolla tubes cylindrical, forming a distinctly swollen portion around anthers, 2–3 cm long; corolla lobes elliptic, red-orange abaxially sparsely hirsute, adaxially papillate. Fruits ellipsoid to obovoid, 1–1.5 × 0.8–0.9 cm, with sparse to dense warts, without vertical ridges, calyces deciduous, hirsute;

mesocarp 0.3–0.6 mm thick; fruiting pedicels 2–4 mm, densely hirsute; seeds 0.6–0.7 × 0.67–0.8 mm; exotesta cells with 2 to 5 pores on the inner tangential walls, tuberculate thickenings slightly prominent.

Phenology. *Mussaenda milleri* has been observed to flower in March, with fruiting August to September.

Distribution and habitat. *Mussaenda milleri* is endemic to the province of Nueva Ecija, Luzon, in the Philippines. It has been collected from mid-altitude disturbed forest at an altitude of 1065 m.s.m. *Mussaenda milleri* is one of the few Philippine species found at high altitudes above 1000 m.s.m. and appears to be rare.

IUCN Red List category. *Mussaenda milleri* is assessed as Critically Endangered or CR D, with a very small population size estimated to number fewer than 50 mature individuals. *Mussaenda milleri* is considered the most threatened and rare among Philippine *Mussaenda* species due to its restricted population on Mount Umingan (Nueva Ecija). A continuing decline is projected in the area of occupancy and quality of habitat as logging activities by local indigents is evident.

Discussion. *Mussaenda milleri* is a poorly known species known only from the type represented by fruiting material. It is easily recognized by its reddish brown trichomes on the vegetative parts and inflorescences, by the small elliptic to ovate leaves to 12 cm with few lateral vein pairs (five to 11), and by the orange-red, abaxially hirsute corolla lobes. The holotype (*Elmer 22694*, Camp Labi, “summit mountain ridge,” Elmer, 1939: 3780) was destroyed at PNH during World War II. Jayaweera (1964: 122) did cite NY and US duplicates for *Ramos & Edaño 26468* as “nearest to the original description,” which was also collected from the vicinity of Camp Labi, and Jayaweera’s taxonomic opinion is followed here. He characterized *M. milleri* as closely similar to *M. nervosa*, primarily due to the abaxially sunken midrib of leaf blades and the deciduous calyces on fruits. However, the two species have divergent types of indumentum in both vegetative and reproductive parts, number of secondary veins, color and shape of corolla lobes, size of seeds, and number of pores on the inner tangential walls of exotesta. *Mussaenda milleri* is characterized by hirsute indumentum, five to 11 pairs of secondary veins, red-orange and elliptic corolla lobes, slightly larger seeds to 0.7 × 0.8 mm, and two to five pores in seed exotesta on the inner

tangential walls. On the other hand, *M. nervosa* has pilose indumentum, 10 to 15 pairs of secondary veins, yellow and ovate corolla lobes, smaller seeds to 0.6×0.4 mm, and four to 12 pores in seed exostesta.

There are only two sheets, both fruiting, of the type collection *Ramos & Edaño 26468* known from NY and US that were available for examination, and the NY sheet is designated as the holotype. Elmer did not provide a Latin diagnosis and the name was invalidly published in 1939, since a Latin diagnosis or description was required after 1 January 1935 (McNeill et al., 2012, Art. 39.1). Further, Elmer's PNH type (*Elmer 22694* from Luzon, collected in March 1937) was destroyed during World War II, and duplicates were evidently not distributed to other herbaria. Elmer's species name is validated herein based on an earlier collection (1916) from approximately the type locality in Luzon. The morphological description of the flower is taken from his description of the destroyed type, which was flowering; however, no flowering material was available to the authors.

14. *Mussaenda multibracteata* Merr., Philipp. J. Sci., 11(Pt. C): 34. 1916. TYPE: Philippines. Sorsogon: Luzon [Bicol region], Mt. Pocdal, $12^{\circ}58'N$, $124^{\circ}01'E$, July–Aug. 1915, *M. Ramos 23585* (lectotype, designated by Jayaweera [1964: 124], NY [barcode] 00132313!; isoelectotypes, A [bc] 00096197 digital image!, K [bc] K000740978 digital image!, US [bc] 000137856 digital image!). Figure 13.

Shrubs or trees, 2–6 m tall; young twigs greenish brown, densely hirsute, the trichomes more than 12-celled, brown; older branches with few to many lenticels, reddish brown, glabrous or with few scattered trichomes. Leaf blades lanceolate to elliptic, or elliptic to ovate, $9.5\text{--}30 \times 4\text{--}16$ cm, membranaceous to subcoriaceous, sparsely to densely hirsute above, densely hirsute, especially on midrib and veins underneath; margins ciliate; apex acuminate, not conduplicate; base cuneate or long attenuate; secondary veins in 8 to 11 pairs, prominulous above; petioles 1–3 cm long, densely hirsute; stipules triangular, $6.5\text{--}14 \times 5\text{--}7$ mm at the base, persistent or deciduous, abaxially with dense indument, adaxially with dense indument only at the base; apex bifid \pm half to $3/4$ of length, the lobes slightly diverging or not; colleters numerous, in continuous rows or in groups of 2 at the base. Inflorescences spreading or congested, densely hirsute; bracts numerous, lanceolate, entire to trilobed, $5\text{--}13.5 \times 1.5\text{--}2.5$ mm, densely

hirsute underneath, with tuft of trichomes only at the base above; pedicels 0.5–1 mm, with dense, ascending trichomes. Flowers odorless; calyx tubes cup-shaped to shortly tubular, 6–8 mm long, densely hirsute; calyx lobes foliaceous, persistent, not recurved, $20\text{--}27 \times 6\text{--}7$ mm, with distinct median ridge, hirsute on both surfaces, occasionally with a single calycophyll; colleters as 1 or 2 pairs per lobe, in sinuses between calyx lobes; calycophylls with blades ovate or elliptic, 5-nerved, $5.5\text{--}11.7 \times 3\text{--}6.8$ cm, white, sparsely pubescent especially along nerves on both surfaces, margins ciliate, apex acute or acuminate, base cuneate to attenuate; calycophyll stalks 2–3.5 cm, densely hirsute; corolla buds densely hirsute, becoming hirsute only in the upper half and with few scattered trichomes below in open flowers; corolla tubes infundibular, swollen portion around anthers indistinct, 2.5–2.8 cm long, yellowish white, without tuft of trichomes surrounding the opening; short-styled flower morphs with dense, long, unstriated, ribbon-like trichomes internally to the base of anthers from the top; long-styled flower morphs with sparse, short, striate, ribbon-like trichomes internally to short filaments from the top; corolla lobes ovate or broadly elliptic, $5\text{--}6 \times 4\text{--}5$ mm, yellow to orange, abaxially hirsute, adaxially papillate, apex not recurved without filiform apical appendages; stamens inserted to distal $1/4$ in short-styled flower morphs, around middle in long-styled flower morphs, filaments glabrous, anthers linear, 5–5.5 mm in short-styled flower morphs, 6–6.5 mm in long-styled flower morphs, glabrous, apex acute or obtuse; pollen diameters to $14.85\text{ }\mu\text{m}$, apertures 4, rarely 3; ovary $5\text{--}5.5 \times 2\text{--}2.5$ mm, style 3–5 mm in short-styled flower morphs, 18–22 mm in long-styled flower morphs, stigma 1–1.5 mm in short-styled flower morphs, 7–9 mm in long-styled flower morphs, smooth, not recurved and included in long-styled flower morphs. Fruits ellipsoid, $1.7\text{--}2.2 \times 1\text{--}1.2$ cm, with dense warts, without vertical ridges, green, calyces persistent, densely hirsute; mesocarp 1–1.2 mm thick; fruiting pedicels 4–6 mm, densely hirsute; seeds $0.53\text{--}0.67 \times 0.46\text{--}0.56$ mm; exostesta cells with 4 to 11 pores on the inner tangential walls, tuberculate thickenings slightly prominent.

Local names. Langla (Sbl); Tana-tana (Bik), according to Alejandro (pers. obs.).

Phenology. *Mussaenda multibracteata* has been observed to flower in May to November and in fruit from July to August and October to December.



Figure 13. *Mussaenda multibracteata* Merr. —A. Flowering branch. —B. Portion of stem showing stipule. —C. Flower bud. —D. Open anthesal flower. —E. Short-styled flower morph, corolla tube dissected open in longitudinal section. —F. Long-styled flower morph, corolla tube dissected open in longitudinal section. —G. Longitudinal section through ovary. —H. Calyx, style, and stigma of long-styled flower, with the corolla removed. —I. Three fruits, showing persistent calyces. —J, K. Fruit sections showing seed attachments on placentas, in cross and longitudinal sections, respectively. —L. Seed. A–E are taken from *Alejandro 63a* (*Univ. Santo Tomas Hb.*); F–L, from *Alejandro 63b* (US).

Distribution and habitat. *Mussaenda multibracteata* is known from the provinces of Cagayan and Quezon in the Luzon Region of the Philippines. It is also known from the provinces of Camarines Norte, Camarines Sur, Catanduanes, Albay, and Sorsogon in the Bicol region to the southeast. The species has been collected in low- to high-altitude, secondary and primary forests, on riversides, streamsides, on mountainsides, on clay or sand soils, and from altitudes ranging from 150 to 2100 m.s.m.

Discussion. Merrill (1911b: 35) noted two collections, the first “*Bur. Sci. 23585 Ramos*” and a fruiting collection (23715), in the protologue for *Mussaenda multibracteata*. Jayaweera (1964: 124) would later lectotypify the first collection, “NY-lectotype.” As Bureau of Science collections for the flora of the Philippines, duplicates would have been deposited at PNH and were destroyed during World War II.

Mussaenda multibracteata is perhaps the most distinctive species among Philippine *Mussaenda* and is characterized by its deeply bilobed stipules and long calyx tubes to 8 mm long, by its quite large, foliaceous calyx lobes to 13.5×2.5 mm, and by its large fruits (2.2×1.2 cm) with long pedicels to 6 mm. This species is more similar to African *Mussaenda* than to Asian *Mussaenda* in the size and shape of the calyx lobes (e.g., *M. grandiflora* Benth. and *M. erythrophylla*) and morphology of the fruits (e.g., *M. tristigmatica*).

Additional specimens examined. PHILIPPINES. **Albay:** Mayon Volcano, $13^{\circ}15'N$, $123^{\circ}50'E$, *Mendoza 18376* (PNH), *18431* (L, PNH). **Cagayan:** Luzon region, Mt. Dos Cuernas, $17^{\circ}32'N$, $121^{\circ}59'E$, *Ramos 77006* (PNH). **Camarines Norte:** Mt. Kadig, $14^{\circ}07'N$, $122^{\circ}49'E$, *Edaño 40230* (PNH, US). **Camarines Sur:** Mt. Isarog, $13^{\circ}39'N$, $123^{\circ}22'E$, *Alejandro 63a* (BR, NY, PNH, UBT, *Univ. Santo Tomas Hb.*, US, WAG), *63b* (L, NY, UBT, *Univ. Santo Tomas Hb.*, US), *Convocar 2820* (PNH), *Madulid 6831* (MO); Her-it river, *Clemens 17011* (NY), *Edaño 76425* (NY). **Catanduanes:** Bato trail to Viga, $13^{\circ}51'N$, $124^{\circ}18'E$, *Ramos & Edaño 75143* (NY), *75154* (NY); Mt. Tagmasusso, $13^{\circ}38'N$, $124^{\circ}07'E$, *Ramos & Edaño 75159* (NY), *75259* (NY); *Ramos 30262* (US) and *30509* (A). **Quezon:** Tayabas, Casiguran, $14^{\circ}01'N$, $121^{\circ}37'E$, *Ramos & Edaño 45480* (NY). **Sorsogon:** $12^{\circ}57'N$, $123^{\circ}38'E$, *Ramos 23715* (US).

15. *Mussaenda nervosa* Elmer, *Leafl. Philipp. Bot.* 3(Pt. C): 994–996. 1911. TYPE: Philippines. North Cotabato: Mindanao Region, Davao, Todaya, Mt. Apo, $07^{\circ}00'N$, $125^{\circ}16'E$, May 1909, *A. D. E. Elmer 10510* (lectotype, designated by Jayaweera [1964: 125], A [barcode] 00096198!; isoelectotypes, BISH [bc] 1004486 digital image!, BM [bc] 000945225 digital image!, E [bc] 00502303 digital image!,

GH [bc] 00096199 digital image!, K [bc] K000740977 digital image!, L!, MO [bc] 000716935 digital image!, NY [bc] 00132314!, US [bc] 000917557!). Figure 14.

Shrubs 3–3.5 m tall; young twigs green, sparsely pilose, the trichomes less than 12-celled, brown; older branches with few lenticels, grayish brown, glabrous. Leaf blades ovate to elliptic or lanceolate to elliptic, $6\text{--}15 \times 4\text{--}6.7$ cm, membranaceous to subcoriaceous, puberulous on both surfaces, especially on midrib and veins underneath, margins glabrous, apex acuminate or subcaudate, conduplicate, base acute or obtuse; secondary veins in 10 to 15 pairs, midrib and veins distinctly sunken above, including midrib; petioles 0.5–0.9 cm, sparsely pubescent; stipules triangular, $5\text{--}9 \times 3\text{--}4.5$ mm at the base, deciduous, abaxially with dense indument, adaxially with dense indument only at the base, apex bifid 1/4 to 3/4 of length, the stipule lobes slightly diverging or not; colleters few, in groups of 2 at the base. Inflorescences congested, densely pilose; bracts few, linear to narrowly lanceolate, entire or bilobed, $0.7\text{--}1 \times 1\text{--}2$ mm, densely pubescent underneath, with a few scattered trichomes at the base above; flower pedicels 1–2 mm, with densely appressed trichomes. Flowers odorless; calyx tubes cup-shaped to shortly tubular, 3.5–4.5 mm long, densely pilose; calyx lobes linear or subulate, not recurved, $14\text{--}19 \times 1\text{--}1.5$ mm, pubescence only in external median portion, glabrous inside, occasionally with a single calycophyll; colleters as 1 or 2 pairs per lobe, in sinuses between calyx lobes; calycophylls with blades ovate or elliptic to ovate, 5-nerved, $4\text{--}5.5 \times 3\text{--}4$ cm, white or yellowish white, glabrous or with scattered minute trichomes along nerves above, pubescent only on the nerves beneath, margins ciliate, apex acute, base cuneate; calycophyll stalks 0.9–1.5 cm, sparsely pubescent; corolla buds and open flowers densely pilose; corolla tubes cylindrical, forming a distinctly swollen portion around anthers, 2.5–3 cm long, yellowish white, with tuft of trichomes surrounding the opening; short-styled flower morphs with dense, long, unstriate, ribbon-like trichomes internally to the base of anthers from the top; long-styled flower morphs with sparse short, striate, ribbon-like trichomes internally to short filaments from the top; corolla lobes ovate, $5\text{--}7 \times 2.5\text{--}3$ mm, yellow, abaxially pilose, adaxially papillate, apex recurved, with 1–2 mm filiform apical appendages; stamens inserted to distal 1/4 in short-styled flower morphs, around middle in long-styled flower morphs, filaments glabrous, anthers linear, 6.5–7.5 mm in



Figure 14. *Mussaenda nervosa* Elmer. —A. Flowering and fruiting branch. —B. Leaf section showing sunken midrib and veins. —C. Portion of stem, showing stipules. —D. Flower bud. —E. Open anthesal flower. —F. Long-styled flower morph, corolla tube dissected open in longitudinal section. —G. Short-styled flower morph, corolla tube dissected open in longitudinal section. —H. Longitudinal section through ovary. —I. Calyx, style, and stigma of long-styled flower morph, with the corolla removed. —J, K. Fruit sections showing seed attachments on placentas, in cross and longitudinal sections, respectively. —L. Seed. A–F, H–L are taken from *Alejandro 95* (UBT); G, from the isolectotype *Elmer 10510* (L).

short-styled flower morphs, 6–6.5 mm in long-styled flower morphs, glabrous, apex obtuse; pollen diameters to 16.2 μm , apertures 4; ovary 3–4 \times 2 mm, style 5–6 mm in short-styled flower morphs, 16–18 mm in long-styled flower morphs, stigma 2–3 mm in short-styled flower morphs, 8–9 mm in long-styled flower morphs, smooth or papillose, recurved and included in long-styled flower morphs. Fruits globose or ellipsoid, 1 \times 0.8 cm, with dense warts, without vertical ridges, green, calyces deciduous, usually glabrous; mesocarp 0.4–0.6 mm thick; fruiting pedicels 2 mm, glabrous or puberulous; seeds 0.46–0.6 \times 0.36–0.43 mm, exotesta cells with 4 to 12 pores on the inner tangential walls, tuberculate thickenings slightly prominent.

Local name. Buyan (Bgb), according to Alejandro (pers. obs.).

Phenology. *Mussaenda nervosa* has been observed in flowers and fruits in May and November to December.

Distribution and habitat. *Mussaenda nervosa* is endemic to the Mindanao Region in the southern Philippines and is known from the provinces of North Cotabato, Misamis Occidental, and Bukidnon. The species has been collected in evergreen rainforests, or along dry creek valleys bordered by grasslands, on clay or loam soils, and from altitudes of 1000–1350 m.s.m.

Discussion. Elmer (1911: 995) cited only one collection, his “Type specimen 10510,” which Jayaweera (1964: 125) would later lectotypify “A-lectotype; GH, NY, US-isotypes.” Additional isotypes (BISH, BM, E, K, L, and MO) have been found, although Elmer’s type at PNH was destroyed during World War II.

Mussaenda nervosa can be easily recognized by the sunken midribs and secondary veins on the abaxial leaf surface. No other Philippine *Mussaenda* species possesses this character except for the slightly sunken midribs of *M. milleri*. Additionally, *M. nervosa* is distinguished by its sparsely pilose young twigs that become glabrous, by its conduplicate leaves, by its short bracts to 1 mm long, and by the presence of trichomes only on the median external surface of the calyx lobes. This species is distantly similar to *M. philippinensis* by its long calyx lobes to 19 mm that cover the entire corolla before anthesis and extend to three quarters of the corolla in open flowers (vs. calyx lobes to 15 mm and cover three quarters of the corolla before anthesis and more or

less half of the corolla in open flowers in *M. philippinensis*). Also, the fruit calyces are deciduous in *M. nervosa*, whereas they are persistent in *M. philippinensis*.

Additional specimens examined. PHILIPPINES. **Bukidnon:** Kitanglad Mtn. Range, Mt. Kitanglad, 08°74’N, 124°55’E, *Alejandro 10049* (A, L, PNH, *Univ. Santo Tomas Hb.*), Sumilao Mun., Brgy. Lupiagan, 08°11’N, 124°55’E, *Ingle & Baylomo 630* (A). **Misamis Occidental:** Mindanao Region, Mt. Malindang, 08°16’N, 123°37’E, *Alejandro 95* (UBT, *Univ. Santo Tomas Hb.*).

16. *Mussaenda palawanensis* Merr., Philipp. J. Sci., 10(Pt. C): 103. 1915. TYPE: Philippines. Palawan: Palawan Island, Point Separation, 09°06’N, 118°07’E, July 1912, *E. Fénix 15531* (lectotype, designated by Jayaweera [1964: 127], US [barcode] 000424851!; isolecotype, K [bc] K000740976 digital image!). Figure 15.

Shrubs 2–3 m tall; young twigs green, pilose, the trichomes less than 12-celled, brown; older branches with few lenticels, reddish brown, glabrous. Leaf blades narrowly elliptic to ovate or obovate, 7–22 \times 3.5–7.5 cm, membranaceous to subcoriaceous, variably pubescent on both sides, especially on midrib and veins underneath, margins ciliate, apex abruptly acuminate, not conduplicate, base obtuse or cuneate to attenuate; secondary veins in 9 to 14 pairs, prominulous above; petioles 0.5–0.9 cm, densely pubescent; stipules triangular, 8–11.5 \times 5–7 mm at the base, persistent or deciduous, abaxially with dense indumentum, adaxially with dense indument only at the base; apex bifid \pm half its length, the stipule lobes slightly diverging or not; colleters numerous, in groups of 2 at the base. Inflorescences congested, densely pilose to glabrate; bracts few, linear to narrowly lanceolate, entire or bilobed, 3.5–10 \times 1–1.8 mm, sparsely pubescent underneath, glabrous or sparsely pubescent above. Flowers 5-merous, rarely 6-merous, odorless; flower pedicels 0.5–1 mm, with densely appressed trichomes; calyx tubes cup-shaped to shortly tubular, 4–5.8 mm long, densely pilose; calyx lobes lanceolate or subulate, not recurved, 8–14 \times 1–2.5 mm, pilose on both sides, occasionally with a single calycophyll; colleters as 2 to 4 pairs per calyx lobe, in sinuses between calyx lobes; calycophylls ovate, 5-nerved, 6–8.2 \times 4–6 cm, white or cream, sparsely pubescent on the nerves of both surfaces, margins ciliate, apex acuminate, base cuneate, stalks of calycophylls 0.8–1.4 cm, densely pubescent; corolla buds densely pilose, usually remaining pilose all over or only on the



Figure 15. *Mussaenda palawanensis* Merr. —A. Flowering branch. —B. Portion of stem with stipule. —C. Flower bud. —D. Open anthesal flower. —E. Short-styled flower morph, corolla tube dissected open in longitudinal section. —F. Long-styled flower morph, corolla tube dissected open in longitudinal section. —G. Longitudinal section through ovary. —H. Calyx, style, and stigma of long-styled flower morph, with the corolla removed. —I. Portion of fertile axis with four fruits. —J, K. Fruit sections showing seed attachments on placentas, in cross and longitudinal sections, respectively. —L. Seed. A–E are taken from *Alejandro 77* (*Univ. Santo Tomas Hb.*); F–L, from *Alejandro 78* (UBT).

upper half and with few scattered trichomes below in open flowers; corolla tubes infundibular, swollen part around anthers indistinct, 2.8–3.2 cm long, yellowish white or cream, with tuft of trichomes surrounding the opening; short-styled flower morphs with densely long, unstriated, ribbon-like trichomes internally to the base of anthers from the top; long-styled flower morphs with sparsely short, striate, ribbon-like trichomes internally to the short filaments from the top; corolla lobes ovate, 5–10 × 3–3.5 mm, yellow-orange, abaxially pilose, adaxially papillate or puberulous, apex not recurved, with 2–2.5 mm filiform apical appendages; stamens inserted to distal 1/4 in short-styled flower morphs, around middle in long-styled flower morphs; filaments glabrous; anthers linear, 5–6 mm in short-styled flower morphs, 4.5–5 mm long in long-styled flower morphs, glabrous, apex acute; pollen diameters to 18.45 µm, apertures 4, rarely 3; ovary 4 × 2–2.5; style 6–8 mm in short-styled flower morphs, 19–22 mm in long-styled flower morphs; stigma 4–4.5 mm in short-styled flower morphs, 7–8 mm in long-styled flower morphs, smooth, recurved, included or semi-exserted in long-styled flower morphs. Fruits globose or ellipsoid, or obovoid, 1.2–2 × 0.9–1.4 cm, with dense warts, without vertical ridges, green, sparsely pubescent, calyces deciduous, sparsely pubescent; mesocarp 0.7–1.1 mm thick; fruiting pedicels 2–5 mm, sparsely pubescent; seeds 0.6–0.77 × 0.73–0.83 mm; exotesta cells with 3 to 8 pores on the inner tangential walls, tuberculate thickenings slightly prominent.

Local names. Bayan (Pal); Boyon (Tbw); Buyan (Pal); Malabuyon (Tag), according to Alejandro (pers. obs.).

Phenology. *Mussaenda palawanensis* has been collected in flower from February to July and in fruit March and July to August and November to December.

Distribution and habitat. *Mussaenda palawanensis* is considered to be restricted to Palawan Island and is known from Palawan and Taytay Provinces, but populations have extended to Quezon Province in the Calabarzon Region to the north and Maguindanao Province in Mindanao to the east, extending to Palmas Island, the southernmost island now in North Sulawesi, Indonesia. The species has been collected from low-altitude, occasionally mid-altitude, secondary forests, on mountainsides, on streamsides, on disturbed roadsides, on clay or sandy soils and occasionally

ultramafic soils, and from altitudes ranging from 25 to 750 m.s.m.

Discussion. Merrill (1915: 103) mentioned only the one collection, “*Bur. Sci. 15531 Fénix* (type),” in his protologue for *Mussaenda palawanensis*. As a Bureau of Science collection for the flora of the Philippines, one duplicate would have been deposited at PNH and destroyed during World War II. The surviving duplicate at US was identified as “US-lectotype” in Jayaweera’s treatment of Philippine *Mussaenda* (1964: 127). An additional isoelectotype at K has also been found.

Mussaenda palawanensis is characterized by the long filiform appendages to 2.5 mm at corolla apices and the thick mesocarp to 1.1 mm of the fruit. Variability within *M. palawanensis* occurs in the density of trichomes on young twigs; size, shape, and indumentum of leaves and bracts; and divergence of the stipules. *Mussaenda palawanensis* resembles *M. philippica* var. *philippica* in the morphology of vegetative parts and *M. nervosa* based on the morphology of flowers and type of indumentum. In these three species, the size of calyx lobes is valuable for their distinction. *Mussaenda nervosa* has the longest calyx lobes (14–19 mm), followed by *M. palawanensis* (8–14 mm), and the shortest ones are found in *M. philippica* var. *philippica* (1.5–3.5[–5.5] mm). *Mussaenda palawanensis* is restricted and observed to be more common in Palawan than *M. philippica* var. *philippica*.

Additional specimens examined. PHILIPPINES. **Maguindanao:** Nara Mun., vic. Trident mine, Victoria range, 09°23’N, 118°24’E, *Soejarto & Madulid 6144* (L). **Palawan:** Puerto Princesa, Santa Lourdes, 09°47’N, 118°45’E, *Alejandro 77* (BR, L, *Univ. Santo Tomas Hb.*), 78 (BR, L, UBT), Bacungan, 09°54’N, 118°42’E, *Alejandro 72* (UBT, *Univ. Santo Tomas Hb.*, US), 73 (NY, UBT, US), 75 (L), 76 (BM, BR), Palawan State University, 09°46’N, 118°44’E, *Alejandro 66* (UBT), 67 (WAG), 68 (BM), *Kondo & Edaño 36685* (PNH), Baraki, 09°26’N, 118°31’E, *Fox 13354* (A); Tindogan Distr., Mantalingajan Mt. Range, Mt. Cantung, 08°59’N, 117°49’E, *Pipoly et al. 37956* (A, NY); Batarasa, Marangas River, 08°41’N, 117°39’E, *Alejandro 82* (PNH), 83 (PNH), 84 (*Univ. Santo Tomas Hb.*); Panacan Aborlan, Victoria Mtns., 09°00’N, 118°00’E, *Sulit 12343* (PNH); Mt. Ibugi, *Ebalo 67441* (PNH), *Ebalo & Conklin 1227* (A); Debangan Island, near Taytay, 10°49’N, 119°30’E, *Merrill 11526* (US); Balabac Island, 07°58’N, 117°02’E, *Mangubat 481* (NY, US), *Ramos & Edaño 49660* (BR). **Quezon:** Amapaplot, 09°14’N, 117°59’E, *Espiritu 91473* (PNH), Mono, *Reynoso 87760* (PNH), underground, *Cordero & Espiritu 91572* (L, PNH). **Taytay:** Taytay Mun., 10°49’N, 119°30’E, *Ridsdale 156719* (PNH); Brooke’s Point, 08°46’N, 117°50’E, *Edaño 244* (A, PNH); Dalupaon, Paracao, *Bourell 2244* (A, MO, US); San Antonio Bay, 08°39’N, 117°32’E, *Merrill 867* (US). INDONESIA. **North Sulawesi:** Palmas Island [Miangas], *Merrill 5338* (NY).

17. *Mussaenda philippica* A. Rich., Mém. Soc. Hist. Nat. Paris 5: 245. 1834. TYPE: Philippines. Nat. Capital Region: Manila, 1819, *G. S. Perrottet s.n.* (holotype, P [barcode] P000237778!).

Shrubs or trees 1.5–8 m tall; young twigs green to grayish brown, glabrous or puberulous, rarely pilose, the trichomes less than 12-celled, white to brownish white; older branches with few to many lenticels, reddish or grayish brown, glabrous. Leaf blades elliptic to ovate, or obovate, $3.5\text{--}23.5 \times 2\text{--}12$ cm, membranous to subcoriaceous, glabrous or pubescent on both sides, especially on midrib and veins underneath, margins glabrous or ciliate, rarely slightly sinuate, apex acuminate or subcaudate, rarely conduplicate, base cuneate or long attenuate; secondary veins in 6 to 15 pairs, prominulous above; petioles 0.2–5 cm, glabrous or pubescent; stipules triangular, or ovate, $3\text{--}12 \times 2\text{--}7$ mm at the base, persistent or deciduous, abaxially glabrous to puberulous, or pubescent, adaxially pubescent all over or only at the base, apex bifid $1/8$ to $3/4$ of length, the stipule lobes slightly diverging or not; colleters few or numerous, in continuous rows or in groups of 2 at the base. Inflorescences spreading or congested, glabrous or puberulous, rarely densely pilose; bracts few, linear, lanceolate, or ovate, entire to trilobed, $2.5\text{--}5 \times 0.8\text{--}1.7$ mm, pubescent underneath, glabrous above. Flowers odorless; flower pedicels 1–3 mm, with appressed or ascending trichomes; calyx tubes cup-shaped to shortly tubular, 3.5–5 mm long, glabrous or pubescent; calyx lobes lanceolate or subulate, rarely recurved, $1.5\text{--}3.5(-7) \times 1.5\text{--}2$ mm, pubescent outside, glabrous or pubescent inside, occasionally with a single calycophyll or all developed into calycophylls; colleters as 1 to 4 pairs per lobe, in sinuses between calyx lobes; calycophylls elliptic to ovate or orbicular, 5-nerved, $3.5\text{--}13 \times 2\text{--}8.5$ cm, white or cream, glabrous or puberulous along venation of both surfaces, margins ciliate or glabrous, apex apiculate or acuminate, base cuneate or attenuate, calycophyll stalks 0.5–2 cm, puberulous or pubescent; corolla buds densely pubescent, remaining pubescent or only on the upper half and with few scattered trichomes below in open flowers; corolla tubes cylindrical, forming a distinctly swollen part around anthers, 1.5–3 cm long, cream or greenish white, with or without tuft of trichomes surrounding the opening; short-styled flower morphs with dense, long, unstriate, ribbon-like trichomes internally to the base of anthers from the top; long-styled flower morphs with short, striate, straplike trichomes internally to the base of anthers or to the short filaments from the top; corolla lobes ovate, 4–8

$\times 2.5\text{--}5$ mm, yellow or yellow-orange, abaxially pubescent, adaxially papillate; apex recurved or not, with 0.5–2 mm filiform apical appendages; stamens inserted to distal $1/4$ in short-styled flower morphs, around middle in long-styled flower morphs, filaments glabrous, anthers linear to lanceolate, 5–6.5 mm in short-styled flower morphs, 5–5.5 mm in long-styled flower morphs, glabrous, apex acute; pollen diameters $15.75\text{--}16.65$ μm , apertures 4, rarely 3; ovary $3.5\text{--}5 \times 1.5\text{--}2.5$ mm, style 3–7 mm in short-styled flower morphs, 10–24 mm in long-styled flower morphs, stigma 1.5–4 mm in short-styled flower morphs, 3–9 mm in long-styled flower morphs, smooth or papillose, recurved or not, included, or semi-exserted in long-styled flower morphs. Fruits globose or ellipsoid, or obovoid, $1\text{--}1.8 \times 0.8\text{--}1.1$ cm, with sparse to dense warts, without vertical ridges, green, dark brown when ripe, calyces deciduous, glabrous or puberulous; mesocarp 0.7–1.1 mm thick; fruiting pedicels 2–5(–7) mm, glabrous or puberulous; seeds $0.45\text{--}0.98 \times 0.35\text{--}0.8$ mm; exotesta cells with 2 to 7 pores on the inner tangential walls, tuberculate thickenings slightly prominent or inconspicuous.

Discussion. Although Jayaweera (1964: 128) identified the type for *Mussaenda philippica* to an unnumbered *Perrottet* collection, he did not include its citation (1964: 129–130) among the many specimens in his taxonomic treatment of the species. The type specimen *Perrottet s.n.* collected in 1819 (*Perrottet*, 1834: 245) was only recently located by the authors at the Paris herbarium.

KEY TO THE VARIETIES OF *MUSSAENDA PHILIPPICA* IN THE PHILIPPINES

- 1a. Young twigs and inflorescences glabrous or puberulous; leaf blades puberulous abaxially, rarely conduplicate at apex; corolla lobes with apical appendages 1 mm or longer.
 - 2a. Calyx tube pubescent; calyx lobes all developed into calycophylls
 - .. 17a. *M. philippica* A. Rich. var. *aurorae* Sulit
 - 2b. Calyx tube puberulous at the most; calyx lobes occasionally with a single calycophyll
 - 17b. *M. philippica* A. Rich. var. *philippica*
- 1b. Young twigs and inflorescences pilose; leaf blades densely pubescent abaxially, strongly conduplicate at apex; corolla lobes with apical appendages less than 1 mm long
 - 17c. *M. philippica* A. Rich. var. *pubescens* Alejandro

17a. *Mussaenda philippica* var. *aurorae* Sulit, Philipp. J. Forest. 2(1): 39, pl. 3, fig. 1. 1939. *Mussaenda philippica* f. *aurorae* (Sulit) Jayaw., J. Arnold Arbor. 45: 131. 1964. TYPE: Philippines. Laguna: Tungtungin, Mt. Balong,

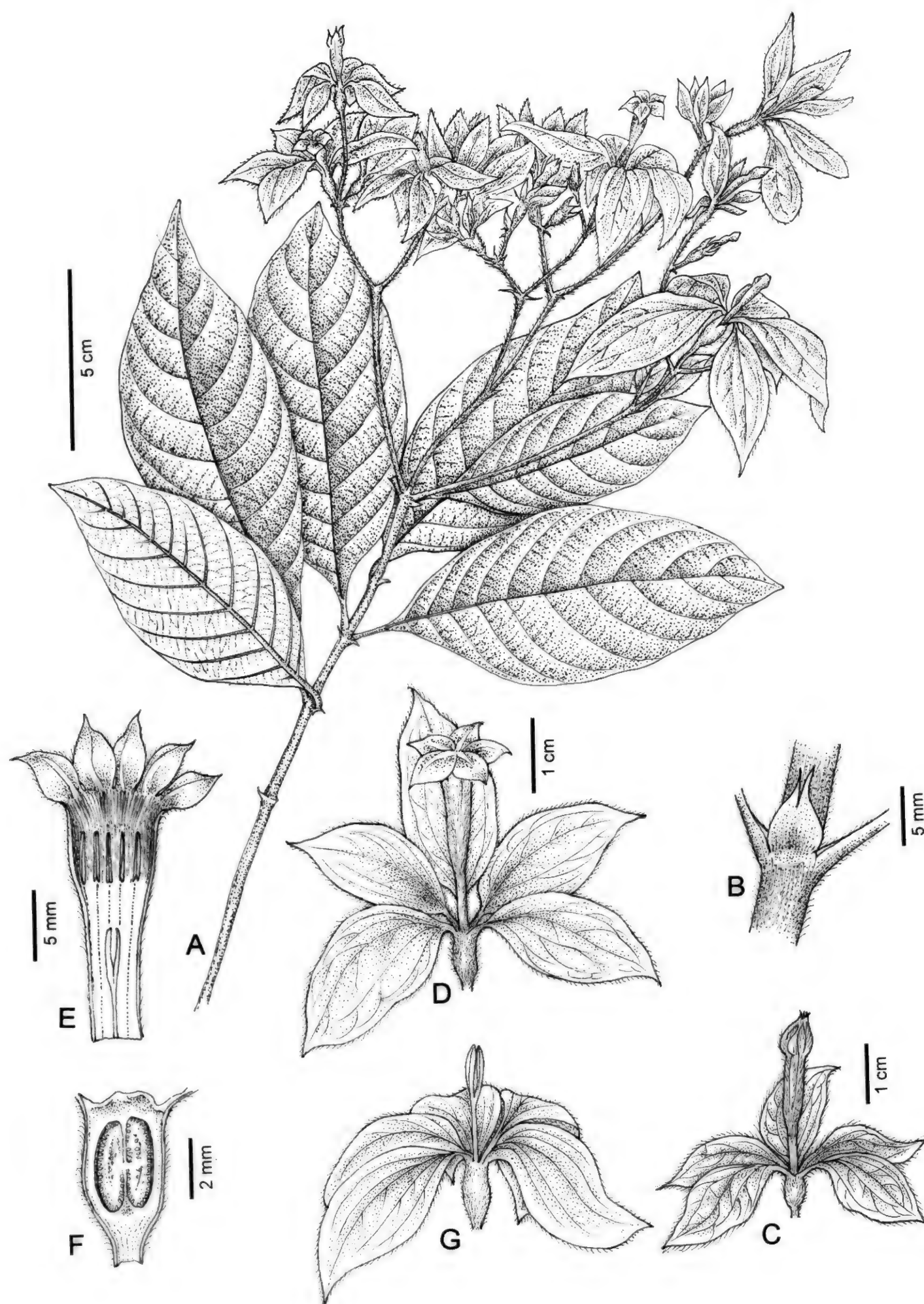


Figure 16. *Mussaenda philippica* A. Rich. var. *aurorae* Sulit. —A. Flowering branch. —B. Portion of stem with stipule. —C. Flower bud. —D. Open anthesal flower, with calyx lobes developed as calycophylls. —E. Short-styled flower morph, corolla tube dissected open in longitudinal section (long-styled flower morph not seen). —F. Longitudinal section through ovary. —G. Calyx, style, and stigma of short-styled flower morph, with the corolla removed. A–G are taken from *Alejandro 9* (UBT).

14°10'N, 121°15'E, July 1915, *C. Mabesa* 24876 (lectotype, designated by Jayaweera [1964: 132], A [barcode] 00295695!; isoelectotypes, L [bc] 00064859!, US [bc] 000137859!). Figure 16.

Shrubs 1.5–3 m tall; young twigs puberulous. Leaf blades 8–16 × 3.2–8.5 cm, puberulous on both surfaces, margins ciliate, apex not conduplicate; secondary in 8 to 10 pairs; petioles 0.7–1.5 cm, sparsely to densely pubescent; stipules triangular, 3.5–7 × 2–5 mm at the base, abaxially with dense indument, adaxially with sparse indument only at the base; apex bifurcate ± half of length, the stipule lobes not diverging. Inflorescences puberulous; bracts entire or bilobed, 3.5–4 × 1–1.7 mm, densely pubescent underneath. Flowers with the pedicels 1–2.5 mm; calyx tubes 3.5–4 mm, pubescent; calyx lobes recurved, all developing into calycophylls; colleter 2 or 3 pairs per lobe; calycophylls 3.5–7 × 2–5.5 cm, puberulous along nerves of both surfaces, margins ciliate, base cuneate; calycophyll stalks 0.6–1 cm, densely pubescent; corolla tubes 1.5–2.3 cm long, with tuft of trichomes surrounding the opening; corolla lobes 4–6 × 4–4.5 mm; apex recurved, filiform apical appendages 1–1.5 mm; anthers 6 mm in short-styled flower morphs; pollen diameters to 15.75 µm; ovary 3.5–4 × 1.5–2 mm, style 3–4 mm in short-styled flower morphs, stigma 3.5–4 mm in short-styled flower morphs; long-styled flower morphs not seen. Fruits not seen.

Local names. Agboy (Myn, Tag); Doña-Aurora; Tawa-tawa (Bkd), according to Alejandro (pers. obs.).

Phenology. *Mussaenda philippica* var. *aurorae* has been observed to flower from May to December (probably throughout the year), but not in fruit.

Distribution and habitat. *Mussaenda philippica* var. *aurorae* is endemic to Laguna, a province in central Luzon, and has also been collected in nearby Manila. This variety is cultivated in Los Baños or is known from secondary forests, on clay, humid soils, and at altitudes ranging from 100 to 250 m.s.m.

Discussion. Jayaweera (1964: 132) selected the type for his new form *Mussaenda philippica* f. *aurorae* as “A–lectotype; US–isotype.” Since then, the authors have identified a second isoelectotype at L.

Mussaenda philippica var. *aurorae* is unique in having five enlarged calyx lobes (3.5–7 × 2–5.5 cm). Exclusive of calycophylls, the variety closely resembles *M. philippica* var. *philippica* in vegetative and

reproductive structures. The variety *aurorae* has been one of the parent taxa of the quite different and colorful Philippine *Mussaenda* cultivars.

Additional specimens examined. PHILIPPINES. **Laguna:** Luzon, Los Baños, University of Philippines, Forestry College, 14°16'N, 121°07'E, *Fosberg* 35018 (L, NY, US), *Steiner* 40038 (PNH), *Walker* 7456 (US), Mt. Makiling, 14°09'N, 121°02'E, *Alejandro* 9 (BR, UBT, *Univ. Santo Tomas Hb.*), *Salvoza* 3215 (PNH). **National Capital Region:** Manila, Manila gardens, 14°35'N, 120°59'E, *Steiner* 22830 (PNH), 82016 (PNH), *Quisumbing* 2101 (PNH).

17b. *Mussaenda philippica* A. Rich var. *philippica*.
Figure 17.

Shrubs or trees 2–8 m tall; young twigs glabrous or puberulous. Leaf blades 3.5–23.5 × 2–12 cm wide, glabrous or puberulous on both surfaces, apex rarely conduplicate, margins slightly sinuate; secondary veins in 6 to 15 pairs; petioles 0.2–5 cm, glabrous or puberulous; stipules 3–11 mm; apex bifurcate 1/4 to 3/4 of length; colleter 2 at the base. Inflorescences glabrous or puberulous; bracts 2.5–5 × 0.8–1.5 mm. Flower pedicels 1.5–3 mm; flowers with calyx tubes 4–5 mm, glabrous or puberulous; calyx lobes usually puberulous and 2–3.5(–5.5) × 1.5–2 mm in long-styled flower morphs, usually glabrous and toothlike or reduced to 2 mm long in short-styled flower morphs, occasionally with a single calycophyll; calycophylls 4–13 × 3–8.5 cm, base cuneate; calycophyll stalks 1.5–2 cm, puberulous; corolla tubes 1.8–3 cm long, with or without tuft of trichomes surrounding the opening, in long-styled flower morphs with sparse trichomes inside; corolla lobes 5–8 × 2.5–5 mm; apex recurved, filiform apical appendages 1–2 mm; pollen diameters to 16.65 µm; ovary 4–5 mm; style 3–7 mm in short-styled flower morphs, 16–24 mm in long-styled flower morphs, stigma 2–4 mm in short-styled flower morphs, 5–9 mm, included or semi-exserted in long-styled flower morphs.

Local names. Agboy (BisPn); Ati-ati (Bis); Ayaw na kilat (Mgd); Ayon-a-kilat (Mar); akawan (MboBl); Balay-lamok, Bali-lamok (Ilk); Balikarap (Tag); Bayoyo, Boyon (BisSL); Buyan-bulagan (Sub); Buyon (BisC, BisSL, Tbw, Tsg); Buyon-buyon (Pal); Darumabi (Mgd); Gatas-birhen (Tag); Gibing-gibing, Gibuyan (Sub); Humbabuyin, Hunbabuyan, Hunbabuyun (Tag); Kahoy-dalaga (Tag); Kambubuyun buladlad (Han); Katuday-bantay (Ilk); Kayum dalaga (SblPn); Labayon (Sub); Langla (Sbl); Mabiyn, Mabiyn-tama (Bng); Makaden (Tbl); Muyon (Mbo); Pulo-pulo (Dgt); Saguyepyep (Ilk); Selimantew (Mbo); Sigidago (Tbw); Taba-taba (Bik); Talig-harap

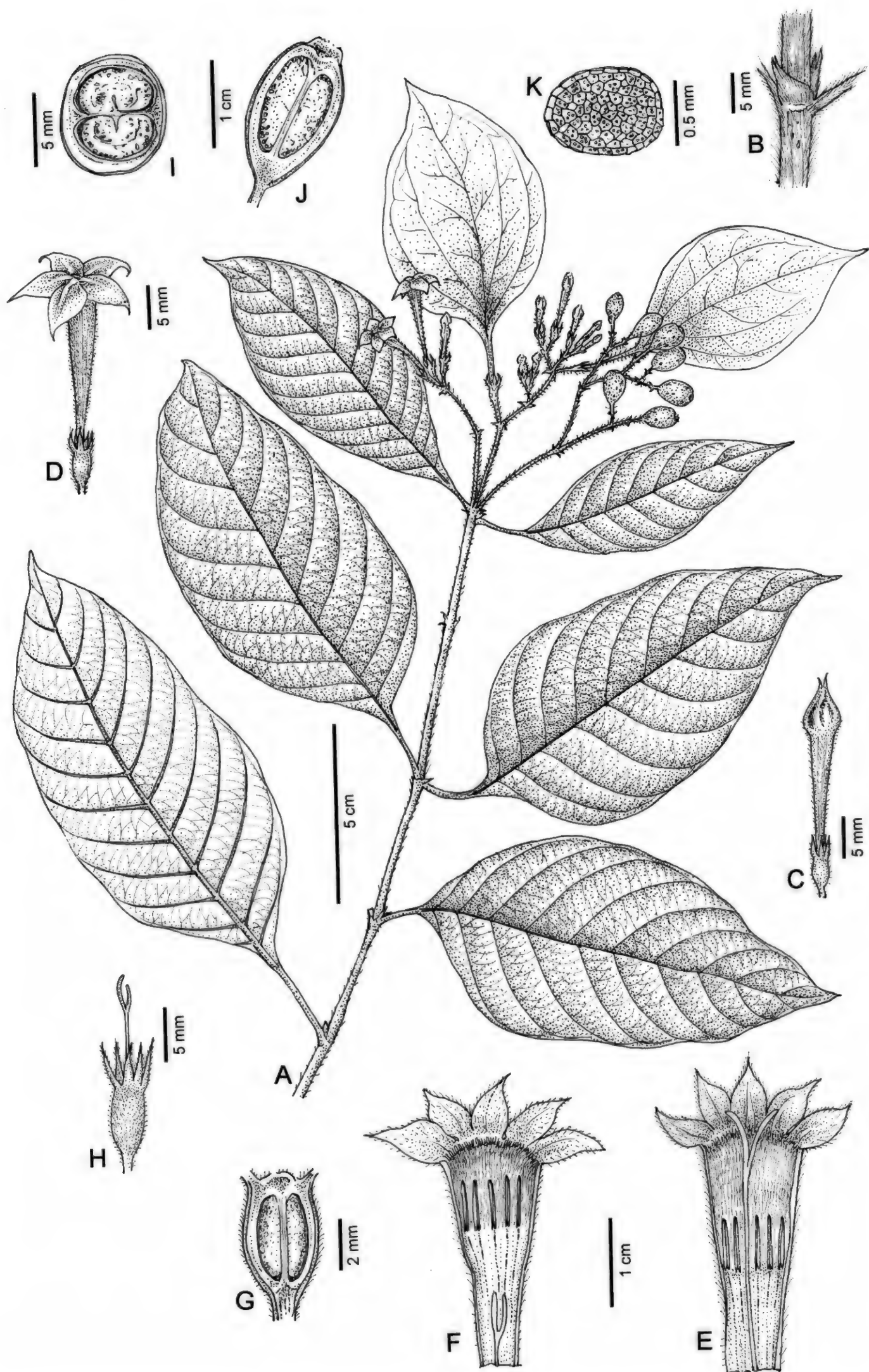


Figure 17. *Mussaenda philippica* A. Rich var. *philippica*. —A. Fertile branch with flowers and fruits. —B. Portion of stem with stipule. —C. Flower bud. —D. Open anthesal flower. —E. Long-styled flower morph, corolla tube dissected open in longitudinal section. —F. Short-styled flower morph, corolla tube dissected open in longitudinal section. —G. Longitudinal section through ovary. —H. Calyx, style, and stigma of short-styled flower morph, with the corolla removed. —I, J. Fruit sections showing seed attachments on placentas, in cross and longitudinal sections, respectively. —K. Seed. A–E, G–K are taken from Alejandro 8 (WAG); F, from Alejandro 7 (UBT).

(Tag); Tangawan (Tas); Tatawatawa (Mbo); Tawa-tawa (Bik, Bkd); Tinga-tinga, Tinulung-gatas (Tag), according to Madulid (2001) and Alejandro (pers. obs.).

Phenology. *Mussaenda philippica* var. *philippica* has been observed in flower throughout the year, with fruiting from January to February, April to June, and August to December.

Distribution and habitat. *Mussaenda philippica* var. *philippica* is widely distributed throughout the Philippines, from the Luzon to Mindanao Regions. In the Philippines, the autonymic variety is known mostly from low to mid-altitudes, occasionally high altitude, in secondary and primary forests, or savanna forests, on coastal scrubs and thickets, on disturbed roadsides, on riversides and streamsides, mostly on clay-loamy or sandy soils, occasionally ultramafic soils, and altitudes range from sea level to 1400 m.s.m.

Discussion. *Mussaenda philippica* var. *philippica* is highly variable in the shape, size, and indumentum of the leaves, stipules, flowers, and fruits. This variety is marked by glabrous to puberulous plant parts and the slightly sinuate margins of the leaves. More often, but not always, the short-styled flower morphs are glabrous and have toothlike or greatly reduced calyx lobes (to 2 mm long) comparable to African species of *Mussaenda* such as *M. isertiana*, *M. microdonta*, and *M. polita* and Asian species such as *M. reinwardtiana*. In contrast, the long-styled flower morphs are puberulous and with longer calyx lobes to 2–3.5(–5.5) mm. *Mussaenda philippica* var. *philippica* is highly similar to *M. pinatubensis* in the puberulent indumentum (or glabrous condition) of vegetative and reproductive parts and also to *M. palawanensis* in the appearance of plant parts. However, *M. philippica* var. *philippica* stipules are bifurcate one fourth to three fourths of their length from the apex (vs. one fourth of length in *M. pinatubensis* and one half of length in *M. palawanensis*), and a more striking contrast is the shorter length of its calyx lobes to 1.5–3.5(–5) mm (vs. 7–8 mm in *M. pinatubensis* and 8–14 mm in *M. palawanensis*). This variety is by far the most frequently collected and widely distributed taxon of the genus in the Philippines. On the other hand, *M. pinatubensis* is restricted to Pampanga and Zambales Provinces (Luzon), while *M. palawanensis* is distributed in the Palawan extending to Quezon and Maguindanao Provinces and to North Sulawesi, Indonesia.

Additional specimens examined. PHILIPPINES. **Agu-san del Norte:** Butuan, Tungao, San Mateo Bo., 08°46'N, 125°37'E, Banzon 128204 (PNH), Mendoza 2009 (PNH), 42398 (PNH, US); Cabadbaran, Mt. Urdaneta, 09°07'N,

125°32'E, Elmer 13301 (NY). **Aklan:** Panay Island, Nabas, Mt. Laserna, 11°49'N, 122°05'E, Alejandro 19 (NY), 33 (PNH, Univ. Santo Tomas Hb.), 34 (PNH), 35 (US, WAG), Buruanga, Brgy. Tigum, Mt. Mangamura, 11°50'N, 121°53'E, Alejandro 41 (NY, Univ. Santo Tomas Hb.), 45 (UBT), 55 (L, PNH), 57 (US), Ibajay, Brgy. Tagbaya, Mt. Bubog, 11°49'N, 122°09'E, Alejandro 21 (BM), 22 (UBT), 23 (US), 24 (NY), 25 (UBT). **Albay:** Bicol region, Mt. Mayon, 13°15'N, 123°40'E, Mendoza 18327 (PNH), 18350 (PNH). **Apayao:** Luzon, Calanasan, Tanglagan, Mt. Duraragan, 16°39'N, 120°29'E, Alejandro 102 (PNH, Univ. Santo Tomas Hb.). **Aurora:** Baler, 14°01'N, 121°35'E, Quisumbing 2054 (PNH), Escritor 21192 (MO); Casiguran, 16°17'N, 122°07'E, Ramos & Edaño 45292 (NY). **Bataan:** Lamao River to Mt. Mariveles, 14°29'N, 120°09'E, Bartlett 14653 (NY, PNH), Borden 1220 (NY, US), Elmer 6673 (NY), Whitford 388 (NY), 524 (NY), Williams 127 (A, NY); Limay, Kuyapo, 14°33'N, 120°35'E, Alejandro 10 (NY), 11 (L), 12 (Univ. Santo Tomas Hb.). **Batangas:** San Juan, Brgy. Hugom, Sitio Biga, 13°46'N, 121°05'E, Alejandro 58 (L, NY), 59 (L, NY). **Bukidnon:** vic. Tanculan, 08°08'N, 124°58'E, Fenix 26030 (NY). **Cagayan:** Babuyan island group, Calayan Island, Mt. Makiling, 19°17'N, 121°27'E, Quisumbing & del Rosario 79792 (PNH); Bagio Cove, 18°06'N, 121°43'E, Allen 150272 (PNH), Lagum, vic. Penablanca, Adduru 218 (MO), Tuguegarao, Bolster 136 (MO), Velasco 24852 (NY), Cuming 1368 (MO); Sulu, 06°59'N, 118°28'E, Mearns 36 (US), 37 (US). **Camarines Norte:** Bicol Nat. Park, 14°05'N, 122°56'E, Canicosa 9765 (PNH), Hallier 1903 (NY). **Camarines Sur:** Carambola, Pili, 13°15'N, 123°48'E, Convocar 2945 (A, MO, PNH); Dalupaon, Paracao, 13°33'N, 122°58'E, Bhern 802 (US), Ahern 818 (US), Bermejos 350 (A, NY, US); Kamugong River, Edaño 75879 (NY); Paracale, Ramos & Edaño 33469 (NY); W slope of Mt. Malinaoc, near Buhi, 13°28'N, 123°33'E Burley 95 (A [2], WAG); Naga City, Panicuason, Mt. Isarog Nat. Park, 13°37'N, 123°10'E, Alejandro 64 (PNH, Univ. Santo Tomas Hb.), Delprete 6458 (NY), Mt. Isarog, 13°39'N, 123°22'E, Merrill 413 (A [2], MO, NY, US), Madulid 6841 (A [2], MO); Nueva Caceres, Vidal 1457 (A [2]). **Capiz:** Libacao, 11°29'N, 122°17'E, Martelino & Edaño 35331 (NY), Edaño 46220 (NY), Dumarao, 11°15'N, 122°40'E, Taleon 33828 (PNH); central Panay, Mt. Kudkuran, 11°09'N, 122°30'E, Jocano 40696 (PNH). **Cotabato:** Bugasan to Parang, 07°24'N, 124°17'E, Edaño 1527 (PNH), S Cotabato, Tasaday, 06°17'N, 124°48'E, Gutierrez & Reynoso 108958 (PNH). **Davao:** Magdug River, 07°22'N, 126°32'E, Edaño 11074 (PNH), Catalnan, 07°04'N, 125°31'E, Kanehira 2497 (NY), Madaum, 07°22'N, 125°48'E, Edaño 1312 (PNH), Santa Cruz, 06°50'N, 125°24'E, Williams 2854 (NY), Davao city, Maa Distr., Langub hills, 07°06'N, 125°37'E, Alejandro 94 (L, PNH), Malagos Watershed Nat. Park, near Phil. Eagle Sanctuary, 07°10'N, 125°27'E, Alejandro 91 (BR, UBT), Todaya Distr., Mt. Apo, 07°00'N, 125°16'E, Alejandro 93 (UBT, Univ. Santo Tomas Hb.), DeVore & Hoover 172 (MO). **Guimaras:** Guimaras Island, Buena Vista Bo., 10°39'N, 122°38'E, Sulit 11804 (PNH). **Ilocos Norte:** Pagudpud, Patapat Mtns., 16°36'N, 120°20'E, Alejandro 103 (UBT), 104 (UBT), 105 (UBT), 106 (UBT, Univ. Santo Tomas Hb.). **Iloilo:** La Rido Hill, Lambunao, 11°32'N, 122°28'E, Reynoso et al. 17905 (A), Gammill 261 (NY, US). **Isabela:** Sierra Madre Mtns., 17°02'N, 122°11'E, Gutierrez 77986 (PNH); Palanan, 17°02'N, 122°25'E, McGregor 10726 (NY). **Laguna:** Los Baños, 14°13'N, 121°08'E, Elmer 8134 (NY), Fosberg 35017 (NY, US), Mendoza 12224

(PNH, US); Mt. Makiling, 11°29'N, 121°08'E, *Elmer 17670* (MO, NY), *Sulit 9747* (PNH); Makiling Nat. Park, *Salvoza 3214* (BR, PNH), U.P.L.B., *Alejandro 7* (UBT, *Univ. Santo Tomas Hb.*), *Price 509* (PNH), *Steiner 40063* (PNH), ca. 100 m outside botanical garden, *Alejandro 8* (WAG), Inst. Pl. Breeding (IPB), *Alejandro 4* (BR), Pangil, 14°24'N, 121°28'E, *Ramos 39882* (PNH, US); Lumban, 14°17'N, 121°27'E, *Demetrio & Mendoza 36232* (PNH); W of Famy, 14°36'N, 121°19'E, *Brenner 2584* (PNH). **Lanao:** Cotabato to Dansalan, 07°12'N, 124°14'E, *Zwickey 34* (NY). **Leyte:** Tacloban, 11°13'N, 124°59'E, *Frohne 35140* (PNH), Palo, 11°08'N, 125°00'E, *Elmer 7045* (NY), *Wenzel 57* (MO), *179* (MO). **Mindoro Oriental:** Mindoro Island, Mansalay, 12°31'N, 121°26'E, *Merrill 912* (MO, NY, US), Mt. Yagaw, E slope, 12°35'N, 121°29'E, *Sulit & Conklin 16840* (PNH), *16875* (PNH), Puerto Galera, Biological Station, 1 Dec. 1953, *Velasquez s.n.* (A); Sablayan, Ligaya, 12°51'N, 120°48'E, *Reed 40835* (PNH). **Misamis Occidental:** Mt. Malindang, 08°17'N, 123°37'E, *Mearn & Hutchison 4716* (NY). **National Capital Region:** Manila, *Deguchi et al. 6303* (MO); Pasig, Blvd., 14°47'N, 121°31'E, *Mendoza 3126* (PNH). **Negros Oriental:** Negros Island, Dumaguete (Cuernos Mtns.), 09°18'N, 123°17'E, *Elmer 10121* (L, MO, NY). **Palawan:** Culion Island, 11°49'N, 119°58'E, *Bermejor 182* (NY, US); Puerto Princesa, Santa Lourdes, 09°47'N, 118°45'E, *Alejandro 79* (UBT), *80* (BM), *Danao 19907* (NY), Mt. Pulgar, 09°44'N, 118°43'E, *Elmer 12792* (A [2], MO, NY), *Cenabre 29149* (A), Irawan, Limpapay, 09°53'N, 118°43'E, *Alejandro 70* (L, US), Impapai forest behind BFD field station, E slope of Mt. Beaufort, *Soejarto & Fernando 7301* (A), Bacungan, 09°54'N, 118°41'E, *Alejandro 74* (UBT, *Univ. Santo Tomas Hb.*); Batarasa, Marangas River, 08°41'N, 117°38'E, *Alejandro 85* (*Univ. Santo Tomas Hb.*); *Curran 4517* (NY, US), *Foxworthy 605* (A, NY, PNH, US), *691* (NY); Taytay, 10°48'N, 119°28'E, *Merrill 9332* (A [2], MO, NY). **Pangasinan:** Umingan, Brgy. Annam, Mt. Umingan, 15°59'N, 120°55'E, *Alejandro 99* (PNH, *Univ. Santo Tomas Hb.*), *100* (*Univ. Santo Tomas Hb.*). **Quezon:** Tayabas, Lucena, 13°56'N, 121°36'E, *Merrill 2890* (NY); Polilio Island, Bo. Balai-balai, 14°50'N, 121°56'E, *Salvoza 3450* (PNH); Karlagan, *Fox 9021* (A, PNH), *Robinson 6847* (L); Alabat Island, Casiguran, 14°07'N, 122°00'E, *Ramos & Edaño 48089* (NY). **Rizal:** Antipolo, 14°34'N, 121°10'E, *Merrill 1341* (NY), *Vidal 389* (A), *Ramos & Edaño 29536* (A); Bosoboso, 14°38'N, 121°14'E, *Merrill 2655* (NY). **Samar:** Baruz, Matuguinao, 12°07'N, 124°53'E, *Gatchalian 15493* (PNH); Pinabacdao, Bo. Obayan, 11°36'N, 124°59'E, *Conese 15797* (PNH); Borongan, Pinamagasan, 11°36'N, 125°26'E, *Castro 5853* (PNH), Tagaslian, 11°33'N, 125°26'E, *Castro 5810* (PNH); Oras, Bantayan, Kadapnan Bo., 12°09'N, 125°25'E, *Castro 5782* (PNH); Laquilacon, 11°47'N, 125°05'E, *Mcgregor 43797* (NY), *Sulit 6125* (PNH); Catamaran, 12°28'N, 124°36'E, *Alcasid & Oane 39863* (PNH), Mt. Cansayao, 12°29'N, 124°37'E, *Sulit 14449* (PNH), Catubig River, 12°34'N, 125°00'E, *Sablava 45* (MO); Tubabao Island, 12°06'N, 125°33'E, *Quisumbing 2045* (PNH); Mt. Purog, *Edaño 15450* (A); Basey, Brgy. Guirang, Sitio Wespel, Sohoton National Park, 11°17'N, 125°40'E, *Alejandro 10164* (*Univ. Santo Tomas Hb.*). **Sorsogon:** Irosin, Mt. Bulusan, 12°42'N, 124°02'E, *Edaño & Gutierrez 37744* (PNH), *38555* (PNH), *Elmer 14388* (MO, NY), Bulusan, Dangkalan, 12°45'N, 124°08'E, *Alejandro 61* (BR, WAG), Mt. Juban, 12°50'N, 123°58'E, *Edaño 37164* (PNH), *37163* (PNH), *Curran 10535* (NY). **Surigao del Sur:** *Ahern 339* (US). **Zambales:** Palauig, Mt. Tapulao, 15°25'N, 119°54'E, *Alejandro 96* (L), *97* (UBT);

Anuling, 15°45'N, 120°03'E, *Ramos & Edaño 44543* (NY); Mt. Pinatubo, 15°07'N, 120°21'E, *Fox 4586* (PNH). **Zamboanga del Norte:** Mindanao, near Kabasalan, Mt. Muralong, 07°47'N, 122°44'E, *Ebalo 718* (PNH), Dikus, 07°48'N, 122°08'E, *Frake 36058* (PNH), *38115* (PNH), Duhinob River, 08°30'N, 123°11'E, *Frake 20332* (PNH).

17c. *Mussaenda philippica* var. *pubescens* Alejandro, var. nov. TYPE: Philippines. Davao Oriental: Mindanao, Mati, 06°57'N, 126°12'E, Mar.–Apr. 1927, *Bureau of Science 49315* (*M. Ramos with G. Edaño*) (holotype, NY [barcode] 00689070!). Figure 18.

Haec varietas ab aliis varietatibus speciei corolla ante anthesin dense pubescente, ramis et axibus inflorescentiarum dense pilosis et apicibus foliorum conduplicatis differt.

Shrubs 6 m tall; young twigs \pm pilose. Leaf blades 4.5–15.5 \times 3.5–8 cm, puberulous above, densely pubescent underneath, margins ciliate, conduplicate, base attenuate; secondary veins in 8 to 12 pairs; petioles 0.2–1 cm, densely pubescent; stipules triangular, 6–12 \times 3–5.5 mm at the base, abaxially with dense indument, adaxially with sparse to dense indument; apex bifurcate 1/8 to \pm half of length, the stipule lobes not diverging; colleters in groups of 2 at the base. Inflorescences congested, densely pilose; bracts 3.5–5 \times 0.8–1.3 mm, densely pubescent underneath, with few scattered trichomes above; flower pedicels 1–2.5 mm, with densely appressed trichomes. Flowers with the calyx tubes 3.5–4.5 mm long, densely pubescent; calyx lobes 5–7 \times 1–1.2 mm, not recurved, pubescent on both sides (denser outside and sometimes only in the lower half), occasionally with a single calycophyll; calycophylls 3.8–8.5 \times 3.5–6.8 cm, puberulous on both sides, especially along the nerves, margins ciliate, base attenuate; calycophyll stalks 0.5–1.4 cm, densely pubescent; corolla tubes 2.3–2.5 cm long, without tuft of trichomes surrounding the opening; long-styled flower morphs with sparsely to densely short trichomes inside; corolla lobes 4–5 \times 3.8–4.2 mm; apex not recurved, filiform apical appendages 0.5 mm; anthers 5–6 mm in short-styled flower morphs, 4–5 mm in long-styled flower morphs; ovary 3–4 \times 2–2.5 mm, style 4.5–5 mm in short-styled flower morphs, 10 mm in long-styled flower morphs, stigma 1.5–2.2 mm in short-styled flower morphs, 3–4 mm, not recurved, included in long-styled flower morphs. Fruits not seen.

Local name. Modelmon (BisC), according to Alejandro (pers. obs.).

Phenology. *Mussaenda philippica* var. *pubescens* has been collected in flower from March to June, but the time of fruiting is not known.



Figure 18. *Mussaenda philippica* A. Rich. var. *pubescens* Alejandro. —A. Flowering branch. —B. Portion of stem with node. —C. Flower bud. —D. Open flower. —E. Short-styled flower morph, corolla tube dissected open in longitudinal section. —F. Long-styled flower morph, corolla tube dissected open in longitudinal section. —G. Longitudinal section through ovary. —H. Calyx, style, and stigma of long-styled flower morph, with the corolla and calyx lobes removed. A–E are taken from the holotype Ramos & Edaño 49315 (NY); F–H, from Edaño 21809 (PNH).

Distribution and habitat. *Mussaenda philippica* var. *pubescens* is known from Agusan del Norte, Camiguin, Davao Oriental, and Negros Occidental. The taxon has been collected at edges of secondary forests and on clay soils. Its altitudinal distribution ranges from 400 to 1300 m.s.m.

IUCN Red List category. *Mussaenda philippica* var. *pubescens* is assessed as Endangered or EN C2a(i) by IUCN (2001) criteria. Population size is estimated to number fewer than 2500 mature individuals and a continuing decline is projected, with no subpopulation estimated to contain more than 250 mature individuals. Most areas occupied by this variety are fragmented forests caused by logging or previous mining activities.

Discussion. *Mussaenda philippica* var. *pubescens* differs from the other two *M. philippica* varieties by its conduplicate leaf apices and dense indumentum on both vegetative and reproductive parts. The pubescence is more prominent in the corolla before anthesis, thus the specific epithet.

Paratypes. PHILIPPINES. **Agusan del Norte:** Butuan, San Mateo Bo., Tungao So., 08°48'N, 125°37'E, *Mendoza 42193* (US). **Camiguin:** 09°13'N, 124°41'E, *Ramos 14604* (US). **Davao Oriental:** Mt. Mayo, 07°00'N, 126°19'E, *Edaño 11384* (PNH), Coronon valley near Santa Cruz, 06°52'N, 125°26'E, *A. N. U. 1564* (A). **Negros Occidental:** Mambanig, Mt. Katugasan, 10°44'N, 123°15'E, *Edaño 21782* (L, PNH), *21809* (PNH).

18. *Mussaenda philippinensis* Merr., Philipp. J. Sci., 3(Pt. C): 264. 1908. TYPE: Philippines. Antique: Semirara Island, July 1905, *E. D. Merrill 4139* (lectotype, designated by Jayaweera [1964: 133], NY [barcode] 00132315!; isoelectotypes, K [bc] K000740975 digital image!, US [bc] 000137860 digital image!). Figure 19.

Shrubs 1–6 m tall; young twigs grayish brown, hirsute, the trichomes more than 12-celled, white to brown; older branches with few lenticels, reddish brown, glabrous. Leaf blades elliptic, 9.5–25 × 3.8–10 cm, membranaceous, puberulous above, densely pubescent especially on midrib and veins underneath, margins ciliate, apex acuminate, not conduplicate, base cuneate or long attenuate; secondary veins in 8 to 12 pairs, prominulous above; petioles 0.5–4.2 cm, densely hirsute; stipules triangular to ovate, 6–13 × 3–4.5 mm at the base, deciduous, abaxially with dense indument, adaxially with sparse indument; apex entire or bifid 1/4 of length, stipule lobes slightly diverging or not; colleters numerous, in continuous rows or in groups of 2 at stipule base. Inflorescences terminal, congested, densely hirsute;

bracts few, linear to narrowly lanceolate, entire or trilobed, 7–18 × 1–1.2 mm, densely pubescent on both surfaces. Flowers odorless; flower pedicels 2–2.5 mm, with densely appressed or horizontal trichomes; calyx tubes cup-shaped to shortly tubular, 3–4 mm, densely hirsute; calyx lobes linear to narrowly lanceolate, not recurved, 10.5–15 × 1–1.2 mm, pubescent outside, glabrous or pubescent inside, usually cover 3/4 of the corolla bud and ± half of the corolla in open flowers, occasionally with a single calycophyll; colleters in 1 to 3 pairs per lobe, in sinuses between calyx lobes; calycophylls with blades ovate to elliptic, 5-nerved, 5–9 × 3–6.5 cm, white, glabrous or with scattered minute trichomes along nerves of both surfaces, margins ciliate, apex acute, base cuneate, calycophyll stalks 1.5–2.3 cm, densely pubescent; corolla buds densely hirsute, remaining hirsute all over or only on the upper half and with few scattered trichomes below in open flowers (sometimes glabrate); corolla tubes infundibular, swollen part around anthers indistinct, 2–3.2 cm long, yellowish white, without tuft of trichomes surrounding the opening; long-styled flower morphs with sparse, short, striate, ribbon-like trichomes internally to the short filaments from the top; short-styled flower morphs not seen; corolla lobes ovate, 4–7 × 2–5 mm, yellow, abaxially hirsute, adaxially papillate, apex recurved, filiform apical appendages absent; stamens inserted around the middle in long-styled flower morphs; filaments glabrous; anthers linear, 3.5–4 mm in long-styled flower morphs, glabrous or with few scattered trichomes, apex acute; pollen diameters to 14.85 µm, apertures 4; ovary 3–3.5 × 1.7–2 mm, style 19 mm in long-styled flower morphs, stigma 6.5 mm, smooth, not recurved, included in long-styled flower morphs. Fruits subglobose, or ellipsoid, 1–1.5 × 0.7–0.8 cm, smooth, without warts and vertical ridges, green, calyces persistent, densely hirsute; mesocarp 0.3–0.6 mm thick; fruiting pedicels 4–5 mm, densely hirsute; seeds 0.6–0.67 × 0.46–0.6 mm; exotesta cells with 3 to 10 pores on the inner tangential walls, tuberculate thickenings slightly prominent.

Local names. Kambubuyon-dariit (Han), according to Alejandro (pers. obs.).

Phenology. *Mussaenda philippinensis* has been collected in flower from May to July and in fruit during June.

Distribution and habitat. *Mussaenda philippinensis* is known from the provinces of Antique, Apayao, Oriental Mindoro, and Palawan, from islands in the central Philippines. It has been collected in low-altitude secondary forests, on ridges and creekside,

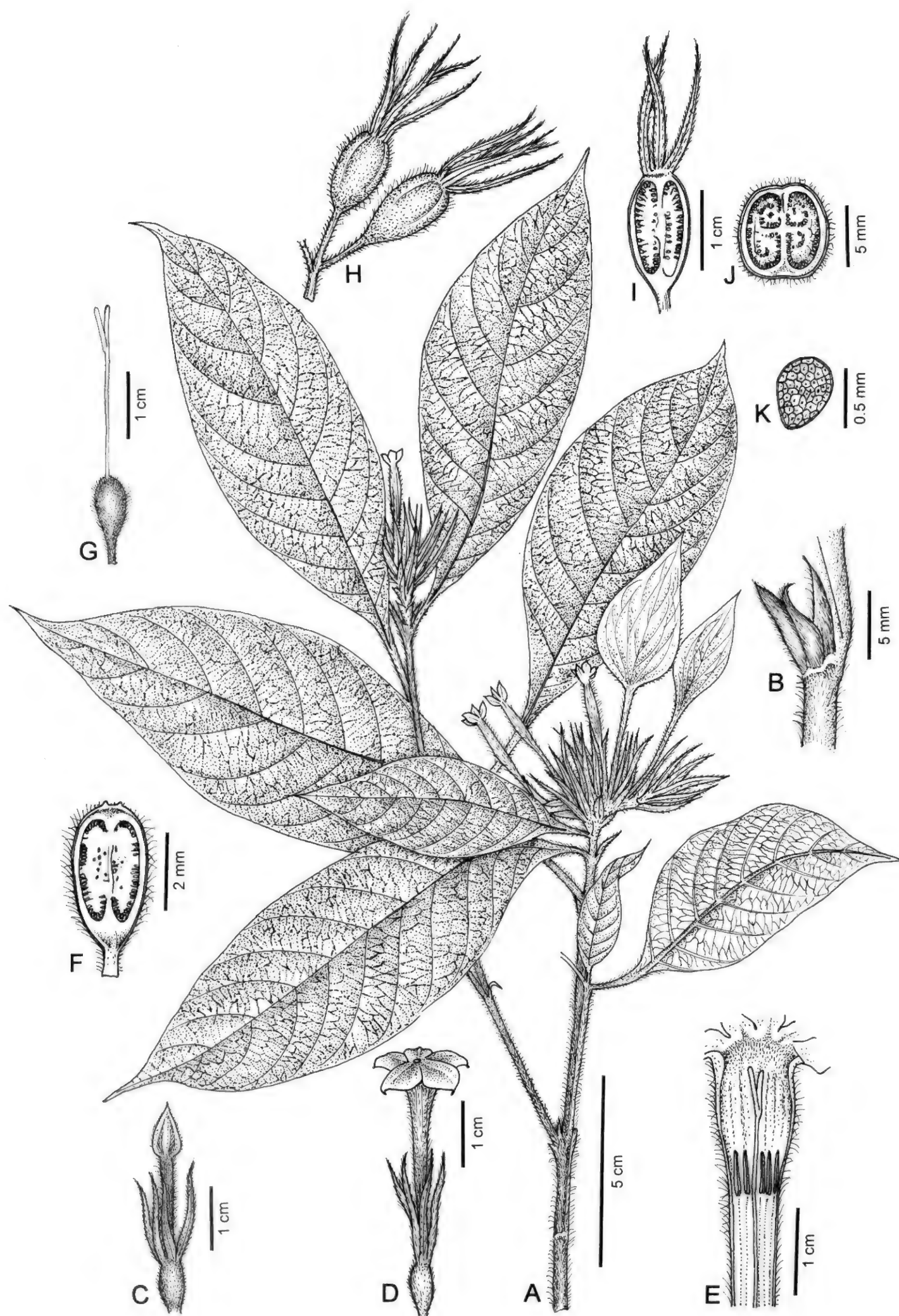


Figure 19. *Mussaenda philippinensis* Merr. —A. Flowering branch. —B. Portion of stem with stipule. —C. Flower bud. —D. Open anthesal flower. —E. Long-styled flower morph, corolla tube dissected open in longitudinal section (short-styled flower morph not seen). —F. Longitudinal section through ovary. —G. Calyx, style, and stigma of long-styled flower, with the corolla and calyx lobes removed. —H. Fruits showing persistent calyces. —I, J. Fruit sections showing seeds on placentas. —K. Seed. A–D are taken from *Sulit & Conklin 17652* (PNH); E–K, from *Edaño 19875* (PNH).

and on clay-loamy soils. Its known altitudinal distribution is from 250 to 300 m.s.m.

Discussion. Merrill referred to only one of his collections in the protologue for *Mussaenda philippensis*, and Jayaweera (1964: 132) accepted this collection (Merrill 4139) as type. As a Bureau of Science collection for the flora of the Philippines, one duplicate would have been deposited at PNH and destroyed during World War II. The duplicate at NY was lectotypified by Jayaweera (1964: 133), and additional isoelectotypes (K and US) have also been found.

This species is characterized by its long, narrow, persistent calyx lobes, congested inflorescences with long bracts, presence of scattered trichomes on the anthers, and densely hirsute fruits. *Mussaenda philippinensis* is closely similar to *M. wrayi* King of the Malay Peninsula, also recognized by Merrill (1908) and Jayaweera (1964), by its persistent calyces. In the Philippine species, it resembles *M. acuminatissima* rather than *M. magallanensis* as suggested by Jayaweera (1964).

Additional specimens examined. PHILIPPINES. **Apayao:** Luzon Region, Mt. Duraragan, 18°14'N, 122°02'E, *Edaño* 19875 (L, PNH). **Mindoro Oriental:** Mansalay, Mt. Yagaw (eastern slope), 12°31'N, 121°26'E, *Ebalo* 193 (PNH), *Paniza* 9436 (PNH), *Sulit & Conklin* 17652 (PNH). **Palawan:** Calamian island group, Culion Island, 11°50'N, 119°58'E, *Bartlett* 15545 (PNH).

19. *Mussaenda pinatubensis* Elmer, Leaflet. Philipp. Bot. 9: 3210. 1934. TYPE: Philippines. Pampanga: Luzon Region, Camp Stotsenburg, Mt. Pinatubo, 15°08'N, 120°20'E, May 1927, A. D. E. Elmer 21978 (holotype, PNH!; isotypes, A [barcode] 00096201 digital image!, G [bc] 00436405 digital image!, GH [bc] 00096200 digital image!, GH [bc] 00096201 digital image!, K [bc] K000740979 digital image!, L [bc] 00057593!, MICH [bc] 1108212 digital image!, MO [bc] 002246678!, NY [bc] 00132316!), P [bc] 02273427 digital image!, US [bc] 000344720 digital image!). Figure 20.

Shrubs or trees, 3–6 m tall; young twigs greenish brown, glabrous; older branches with few to many lenticels, grayish white, glabrous. Leaf blades elliptic, or the young ones orbicular, 3.5–12 × 1.8–4 cm, membranaceous to subcoriaceous, puberulous or with few scattered minute trichomes on both sides, especially on midrib and veins underneath; margins entire, glabrous; apex slenderly acute to acuminate, not conduplicate; base cuneate; secondary veins in 6 to 12 pairs, prominulous above; petioles 0.5–1 cm long, glabrous; stipules triangular

or lanceolate, 5–9 × 2–5 mm at the base, deciduous, abaxially with dense indument, adaxially with sparse indument only at the base; apex bifid 1/4 of length, the lobes slightly diverging or not; colleters numerous, in groups of 2 at the base. Inflorescences congested, glabrous; bracts few, linear-lanceolate, entire or bilobed, 5–6 × 1–1.5 mm, densely pubescent underneath, glabrous or puberulous above. Flowers odorless; pedicels 2–3 mm long, with sparsely appressed trichomes; calyx tubes cup-shaped to shortly tubular, 3–3.5 mm long, sparsely pubescent; calyx lobes linear to lanceolate, not recurved, 7–8 × 0.8–1 mm, pubescent outside, glabrous inside, occasionally with a single calycophyll; colleters as 1 or 2 pairs per lobe, in sinuses between calyx lobes; calycophylls ovate or elliptic, 5-nerved, 5–8 × 2.5–6 cm, yellowish white, glabrous or puberulous on the nerves of both sides; margins glabrous or ciliate; apex acuminate; base cuneate; stalks 0.8–1.7 cm long, puberulous; corolla buds densely pubescent, becoming pubescent only on the upper half and with few scattered trichomes below in open flowers; corolla tubes cylindrical, forming a distinctly swollen part around anthers, 2.4–3 cm long, yellowish white or cream, with tuft of trichomes surrounding the opening; short-styled flower morphs with densely long, unstriated, ribbon-like trichomes internally to the base of anthers from the top; long-styled flower morphs with sparsely to densely short, striated, ribbon-like trichomes internally to the base of anthers or to the short filaments from the top; corolla lobes ovate, 4.5–5 × 4.2 mm, yellow to orange, abaxially pubescent, adaxially papillate; apex not recurved, filiform apical appendages 1–2 mm long; stamens inserted to distal 1/4 in short-styled flower morphs, around the middle in long-styled flower morphs; filaments glabrous; anthers linear, 5–5.5 mm long in short-styled flower morphs, 4–4.5 mm long in long-styled flower morphs, glabrous, apex acute; pollen diameter to 16.2 µm, apertures 4; ovary 3–3.5 × 1.5–2 mm; style 4–4.5 mm long in short-styled flower morphs, 15–17 mm long in long-styled flower morphs; stigma 2–2.5 mm long in short-styled flower morphs, 7–7.5 mm long in long-styled flower morphs, smooth, recurved and included in long-styled flower morphs. Fruits globose or ellipsoid, 1–1.5 × 1 cm, with dense warts, without vertical ridges, green, calyces deciduous, glabrous or puberulous; mesocarp 0.5–0.8 mm thick; pedicels 3–4.5 mm long, glabrous; seeds 0.5–0.73 × 0.38–0.6 mm; exotesta cells with 2 to 5 pores on the inner tangential walls, tuberculate thickenings slightly prominent.

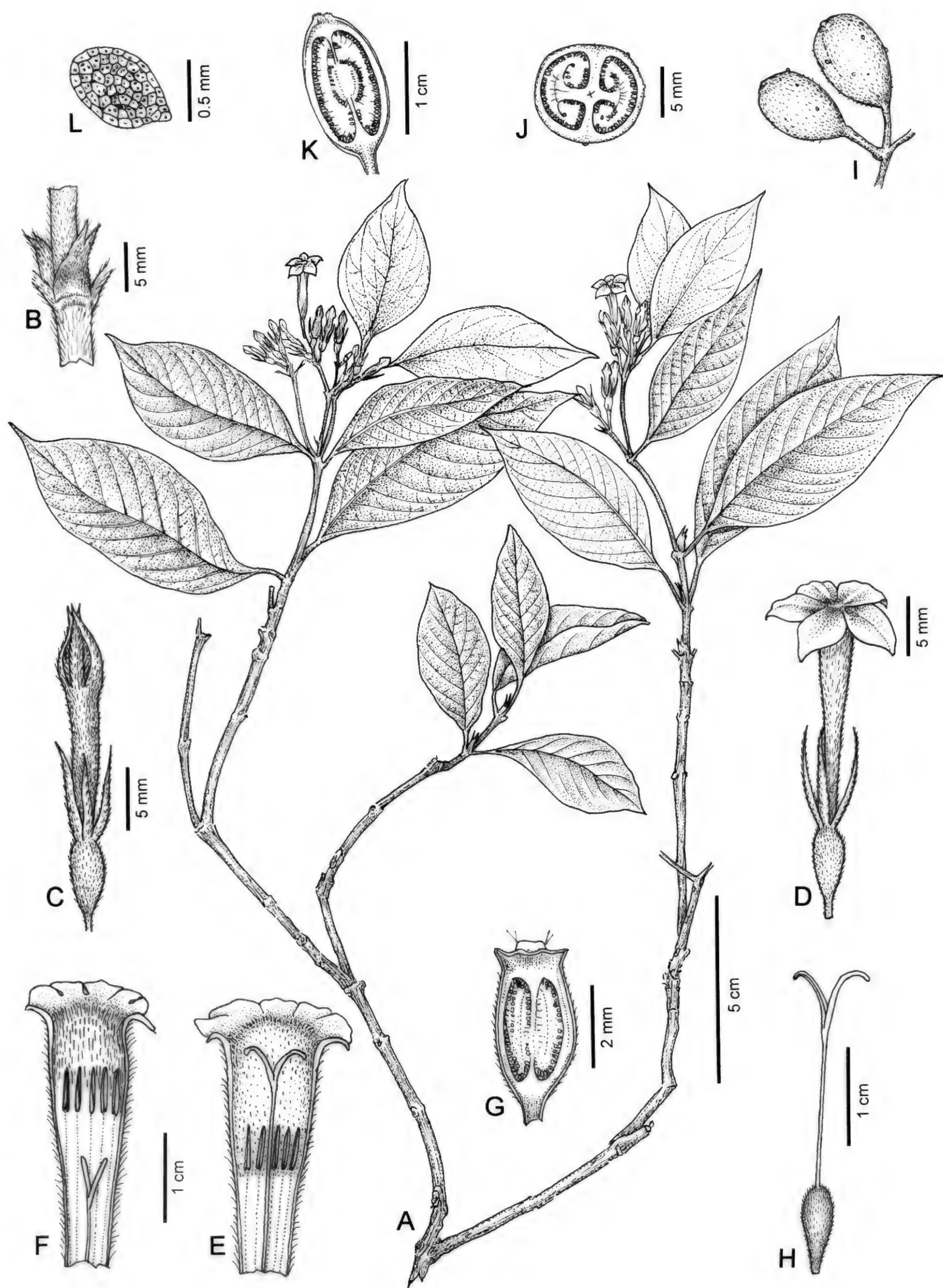


Figure 20. *Mussaenda pinatubensis* Elmer. —A. Flowering branches. —B. Portion of stem with two stipules visible, flanking the node. —C. Flower bud. —D. Open anthesal flower. —E. Short-styled flower morph, corolla tube dissected open in longitudinal section. —F. Long-styled flower morph, corolla tube dissected open in longitudinal section. —G. Longitudinal section through ovary. —H. Calyx, style, and stigma of long-styled flower morph, with the corolla and calyx lobes removed. —I. Two fruits. —J, K. Fruit sections showing seed attachments on placentas, in cross and longitudinal sections, respectively. —L. Seed. A–E are taken from the isotype *Elmer 21978* (NY); F–L, from *Alejandro 1* (*Univ. Santo Tomas Hb.*).

Local name. Kahoy-dalaga (Tag), according to Alejandro (pers. obs.).

Phenology. *Mussaenda pinatubensis* has been observed to flower from May to June and September to November, and in fruit from October to November.

Distribution and habitat. *Mussaenda pinatubensis* is endemic to Pampanga and Zambales Provinces of Luzon. The species has been collected in secondary forests, on riversides, on coastal scrubs, on clay or sandy soils, from sites at elevations from 100 to 1070 m.s.m.

Discussion. According to Jayaweera (1964: 135), the holotype for *Mussaenda pinatubensis* escaped the destruction of the PNH herbarium, “apparently having been on loan during World War II.” This is the only species of Philippine *Mussaenda* with an existing holotype at PNH.

Mussaenda pinatubensis can be easily recognized by its small and congested leaves on the terminals of branches. It is highly similar to *M. philippica* var. *philippica* in the morphology and nearly glabrous vegetative and reproductive parts. However, *M. pinatubensis* differs distinctly by its longer and narrow calyx lobes to $7\text{--}8 \times 0.8\text{--}1$ mm (vs. $1.5\text{--}3.5\text{--}5.5 \times 1.5\text{--}2$ mm in *M. philippica* var. *philippica*), and by its smaller leaves to $3.5\text{--}12 \times 1.8\text{--}4$ cm (vs. $3.5\text{--}23.5 \times 2\text{--}12$ cm in *M. philippica* var. *philippica*).

Additional specimens examined. PHILIPPINES. **Pampanga:** Sapang-bato, $15^{\circ}33'\text{N}$, $121^{\circ}07'\text{E}$, Alejandro 1 (L, NY, PNH, Univ. Santo Tomas Hb., US). **Zambales:** Luzon Island, Botolan, near RMTU (Ramon Magsaysay Tech. Univ.), $15^{\circ}16'\text{N}$, $120^{\circ}02'\text{E}$, 10 Sep. 2002, Alejandro 98 (PNH, Univ. Santo Tomas Hb.), Merrill 2972 (US).

20. *Mussaenda scandens* Elmer, Leaf. Philipp. Bot. 3: 992. 1911. TYPE: Philippines. Davao del Sur: Mt. Apo, $07^{\circ}00'\text{N}$, $125^{\circ}16'\text{E}$, Aug. 1909, A. D. E. Elmer 11291 (lectotype, first designated by Jayaweera [1964: 135], GH, noting isotypes at A, NY, US; subsequent lectotype [cf. Art. 9.17], designated here, GH [barcode] 00096202 digital image!; isolectotypes, A [bc] 00096204 digital image!, BRIT [bc] 23829 digital image!, CAS [bc] 0007125 digital image!, E [bc] 00502302 digital image!, GH [bc] 00096203 digital image!, K [bc] K000740973 digital image!, L [bc] 00057753!, MO [bc] 000716929 digital image!, NY [bc] 00132317!, P [bc] 02273428 digital image!, U [bc] 0227257 digital image!, US [bc] 000917575!). Figure 21.

Shrubs or scandent shrubs, 3 m tall; young twigs green, glabrous; older branches with few to many lenticels, grayish white, glabrous. Leaf blades ovate to broadly elliptic, $6\text{--}14 \times 3\text{--}8$ cm, membranaceous to subcoriaceous, glabrous or puberulous on both sides, especially on midrib and veins underneath; margins glabrous; apex abruptly acute to acuminate, or subcaudate, conduplicate folded; base cuneate to acute; secondary veins in 6 to 10 pairs, prominulous above; petioles 0.3–1.5 cm long, glabrous. Stipules triangular, $7\text{--}8 \times 3.5\text{--}5$ mm at the base, deciduous, abaxially with dense indument, adaxially with sparse indument only at the base; apex bifid 1/4 of length, the lobes slightly diverging; colleters numerous, in continuous rows or in groups of 2 at the base. Inflorescences congested, glabrous; bracts few, lanceolate, entire or trilobed, $4\text{--}11 \times 0.8\text{--}1.2$ mm, densely pubescent underneath, glabrous or puberulous above. Flowers odorless; pedicels 1–1.5 mm long, with sparsely appressed trichomes; calyx tubes extremely reduced, 1.8–2.5 mm long, puberulous; calyx lobes subulate, not recurved, $3.5\text{--}5.5 \times 0.8\text{--}1$ mm, pubescent outside, glabrous inside, occasionally with a single calycophyll; colleters as 1 or 2 pairs per lobe, in sinuses between calyx lobes; calycophylls ovate to elliptic, 5-nerved, $6\text{--}7 \times 3.8\text{--}4.7$ cm, yellowish white, glabrous or with scattered minute trichomes on the nerves of both sides; margins glabrous or ciliate; apex acuminate; base cuneate to obtuse; stalks 1.3–2 cm long, puberulous; corolla buds puberulous, becoming glabrous or puberulous only on the upper half in open flowers; corolla tubes cylindrical, forming a distinctly swollen part around anthers, 2–2.5 cm long, yellowish white, without tuft of trichomes surrounding the opening; short-styled flower morphs with sparsely to densely long, unstriated, ribbon-like trichomes internally to the short filaments from the top; long-styled flower morphs with sparsely short, striated, ribbon-like trichomes internally to the base of anthers from the top; corolla lobes ovate, $2.5\text{--}4 \times 2.5\text{--}3$ mm, yellow, abaxially puberulous, adaxially papillate; apex not recurved, without filiform apical appendages; stamens inserted to distal 1/4 to \pm middle in short-styled flower morphs, around the middle in long-styled flower morphs; filaments with few scattered trichomes; anthers linear, 4–4.5 mm long in short-styled flower morphs, 3.5–4 mm long in long-styled flower morphs, glabrous, apex acute; pollen diameter to $15.75\text{ }\mu\text{m}$, apertures 4; ovary $1.4\text{--}2.3 \times 1.4\text{--}2$ mm; style 3.5–4 mm long in short-styled flower morphs, 13 mm long in long-styled flower morphs; stigma 2–2.5 mm long in short-styled flower morphs, 6 mm long in long-styled flower morphs, smooth, not



Figure 21. *Mussaenda scandens* Elmer. —A. Flowering branch. —B. Portion of stem with stipule. —C. Flower bud. —D. Open anthesal flower. —E. Short-styled flower morph, corolla tube dissected open in longitudinal section. —F. Long-styled flower morph, corolla tube dissected open in longitudinal section. —G. Longitudinal section through ovary. —H. Calyx, style, and stigma of long-styled flower morph, with the corolla and calyx lobes removed. —I. Two fruits, calyces removed. —J, K. Fruit sections showing seed attachments on placentas, in cross and longitudinal sections, respectively. —L. Seed. A–E are taken from Santos 4094 (US); F–L, from the isoelectotype Elmer 11291 (L).

recurved and included in long-styled flower morphs. Fruits ellipsoid, $1\text{--}1.3 \times 0.6\text{--}0.7$ cm, with sparse warts; without vertical ridges, green, calyces somewhat persistent, glabrous; mesocarp $0.4\text{--}0.7$ mm thick; pedicels $3\text{--}5$ mm long, glabrous; seeds $0.83\text{--}0.9 \times 0.67\text{--}0.7$ mm; exotesta cells with 3 to 9 pores on the inner tangential walls, without tuberculate thickenings.

Local name. Buay (Bgb), according to Alejandro (pers. obs.).

Phenology. *Mussaenda scandens* has been observed to be flowering from May, August, and December to February, and fruiting in August, October, and March.

Distribution and habitat. *Mussaenda scandens* is restricted to the provinces of Mindanao. This species is collected in mid-altitudes of submontane forests, thickets, streamsides, clay, and humid soils. Its altitudinal distribution ranges from 750 to 850 m.s.m.

Discussion. Jayaweera (1964) designated the lectotype for *Mussaenda scandens* at GH, but there are two duplicates of the original gathering (*Elmer 11291*) at GH. Applying Article 9.17 (McNeill et al., 2012), the GH material is further discriminated in a subsequent or second step lectotypification, with GH (barcode) 00096202 specified as the lectotype and the second GH sheet as an isoelectotype. This corresponds with Jayaweera's determination labels on both GH sheets. Additional isoelectotypes were found at CAS, E, L, MO, P, and U. For purposes of citation, the more recent author of the second step typification is the one to be cited.

This species is distinct from the rest of Philippine *Mussaenda* species in its climbing habit, grayish white branches at maturity, strongly conduplicate leaves, and greatly reduced calyx tube. *Mussaenda scandens* closely resembles *M. villosa*, also recognized by Jayaweera (1964), found in Thailand, Malaya, Sumatra, and Borneo, primarily due to its habit, vegetative appearance, and glabrous fruits.

Additional specimens examined. PHILIPPINES. **Agu-san del Norte:** Butuan, San Mateo Bo., $08^{\circ}57'N$, $125^{\circ}32'E$, *Mendoza 42053* (PNH). **Basilan:** Basilan City, Lamitan Distr., Univ. Philippines Land Grant, $06^{\circ}39'N$, $122^{\circ}08'E$, *Santos 4094* (US); Zambaonga Distr., Mt. Tubuan, $07^{\circ}03'N$, $124^{\circ}02'E$, *Ramos & Edaño 36596* (L). **Bukidnon:** Mindagat, $08^{\circ}32'N$, $124^{\circ}56'E$, *Pelzer 13555* (PNH). **Davao del Sur:** Todaya Distr., Mt. Apo, $07^{\circ}00'N$, $125^{\circ}16'E$, *Alejandro 92* (L, NY, UBT, *Univ. Santo Tomas Hb.*), Davao, *Copeland 355* (NY, US). **Surigao del Sur:** Mindanao Region, *Wenzel 3354* (BR, MO, NY). **Zamboanga Sibugay:** Malangas, *Ramos & Edaño 37307* (A).

21. *Mussaenda setosa* Merr., Philipp. J. Sci., 10(Pt. C): 104. 1915. TYPE: Philippines. Palawan: Malampaya Bay, Mt. Capoas, $10^{\circ}50'N$, $119^{\circ}13'E$, 21 Apr. 1913, *E. D. Merrill 9496* (lectotype, designated by Jayaweera [1964: 137], US [barcode] 000901285!; isoelectotypes, K [bc] K000740972 digital image!, L!, MO [bc] 000934292!, P [bc] 02273429 digital image!). Figure 22.

Shrubs or trees, 2–4 m tall; young twigs green, hirsute, the trichomes more than 12-celled, white to brown; older branches lenticellate, grayish brown, glabrous or with few scattered trichomes. Leaf blades elliptic to ovate, $12\text{--}29.8 \times 6\text{--}13$ cm, membranaceous, setose on both sides especially on midrib and veins underneath, margins ciliate, apex acuminate or subcaudate, not conduplicate, base cuneate or long attenuate; secondary veins in 15 to 18 pairs, prominent above; petioles $0.5\text{--}3.5$ cm, hirsute; stipules triangular or ovate, $6\text{--}11 \times 4\text{--}6.5$ mm at the base, persistent or deciduous, abaxially with dense indument, adaxially with dense indument only at the base, apex bifid \pm half to $3/4$ of length, stipule lobes slightly diverging or not; colleters numerous, in continuous rows or in groups of 2 at the base. Inflorescences spreading, hirsute; bracts few, lanceolate, entire or trilobed, $3.5\text{--}9 \times 1\text{--}2$ mm, densely hirsute on both sides; flower pedicels $0.5\text{--}1$ mm, glabrous or with few scattered trichomes. Flowers odorless; calyx tubes cup-shaped to shortly tubular, $3\text{--}3.5$ mm, densely hirsute; calyx lobes subulate, not recurved, $4\text{--}6 \times 1$ mm, hirsute outside, glabrous inside, occasionally with a single calycophyll; colleters as 1 or 2 pairs per lobe, in sinuses between calyx lobes; calycophylls ovate to orbicular, 5-nerved, $5.5\text{--}7 \times 4\text{--}5.2$ cm, white, sparsely pubescent along nerves of both surfaces, margins ciliate, apex acuminate, base obtuse; stalks $0.8\text{--}1.6$ cm, densely hirsute; corolla buds densely hirsute, becoming sparsely hirsute only on the upper half in open flowers; corolla tubes cylindrical, forming a distinctly swollen part around anthers, $3\text{--}4$ cm, yellowish or greenish white, with tuft of trichomes surrounding the opening; short-styled flower morphs with dense, long, unstriated, ribbon-like trichomes internally to the base of anthers from the top; long-styled flower morphs with sparsely globular, striate trichomes internally to the short filaments from the top; corolla lobes ovate, $4\text{--}6 \times 3.5\text{--}5$ mm, yellow or yellow-orange, abaxially hirsute, adaxially papillate; apex recurved, filiform apical appendages $1\text{--}1.5$ mm long; stamens inserted to distal $1/4$ in short-styled flower morphs, to basal $1/4$ or around

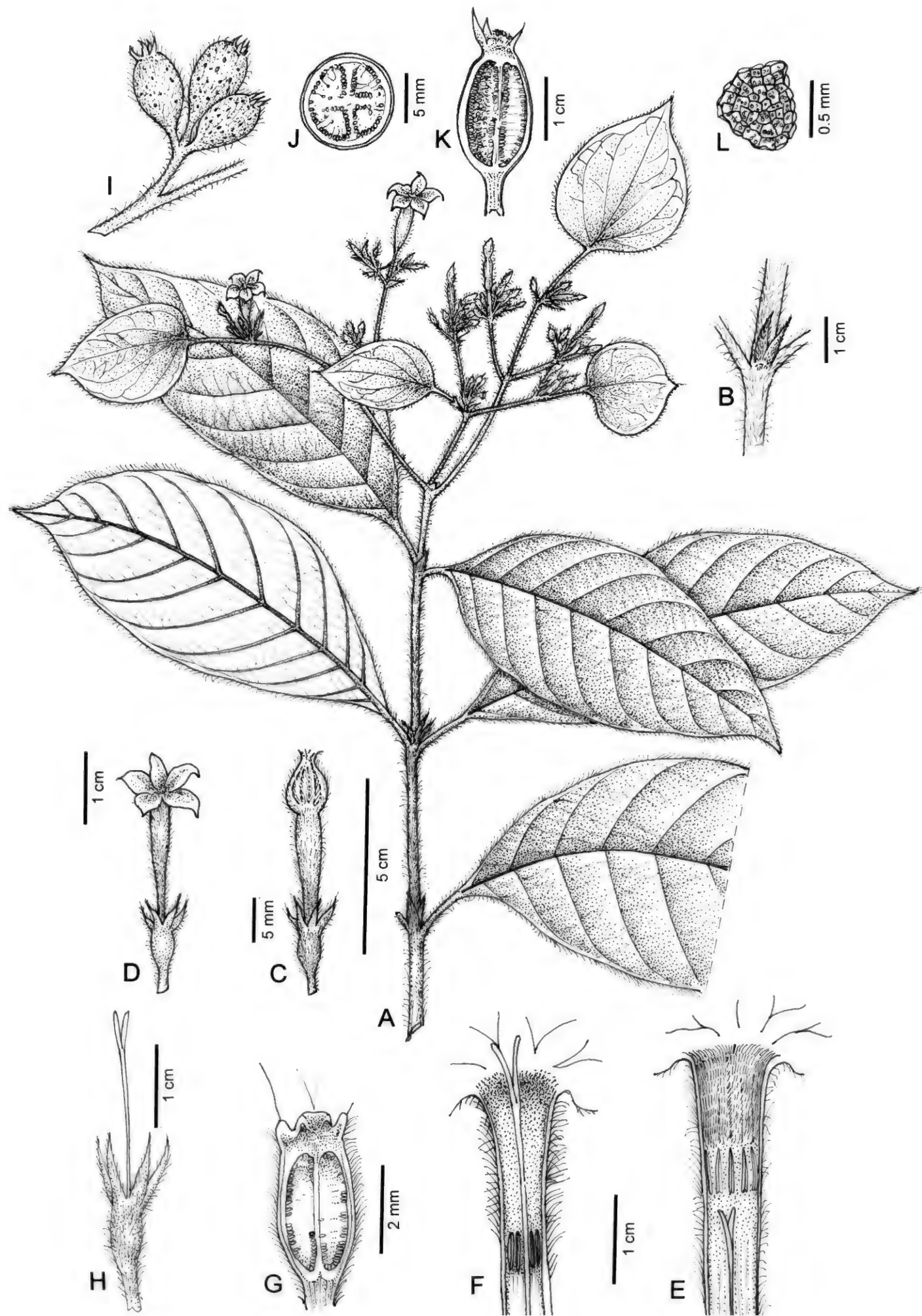


Figure 22. *Mussaenda setosa* Merr. —A. Flowering branch. —B. Portion of stem with stipule. —C. Flower bud. —D. Open anthesal flower. —E. Short-styled flower morph, corolla tube dissected open in section. —F. Long-styled flower morph, corolla tube dissected open in longitudinal section. —G. Longitudinal section through ovary. —H. Calyx, style, and stigma of long-styled flower. —I. Portion of fertile axes with three fruits. —J, K. Fruit sections showing seed attachments on placentas, in cross and longitudinal sections, respectively. —L. Seed. A–D, F–L are taken from *Alejandro 86* (*Univ. Santo Tomas Hb.*); E, from *Alejandro 87* (UBT).

the middle in long-styled flower morphs; filaments glabrous; anthers linear, 5–5.5 mm long in short-styled flower morphs, 3.5–4 mm long in long-styled flower morphs, glabrous, apex acute; pollen diameter to 15.3 μm , apertures 4, rarely 3; ovary $2.5\text{--}3.5 \times 2\text{--}2.5$ mm; style 7–8 mm long in short-styled flower morphs, 19–22 mm long in long-styled flower morphs; stigma 3–3.5 mm long in short-styled flower morphs, 6–7 mm long in long-styled flower morphs, papillose, not recurved and included in long-styled flower morphs. Fruits subglobose, $1.3\text{--}1.6 \times 0.8\text{--}1$ cm, with sparse to dense warts, vertical ridges slightly prominent, green, calyces persistent, sparsely hirsute; mesocarp 0.8–1 mm thick; pedicels 5–6 mm long, densely hirsute; seeds $0.57\text{--}0.78 \times 0.38\text{--}0.85$ mm, exotesta cells with 2 to 5 pores on the inner tangential walls, tuberculate thickenings absent.

Local name. Sigidago (Tbw), according to Alejandro (pers. obs.).

Phenology. *Mussaenda setosa* has been observed to flower from April, and October to December, and in fruit from April, and November to December.

Distribution and habitat. *Mussaenda setosa* is endemic to Palawan, found in low-altitude secondary forests, or dipterocarp forests, on clay-loamy soils, and at altitudes ranging from 40 to 700 m.s.m.

Discussion. Only one collection (Merrill 9496) was cited by Merrill in the 1915 protologue for *Mussaenda setosa*. The destruction of the PNH herbarium during World War II and the PNH type prompted Jayaweera (1964: 137) to lectotypify an isotype at US. Since then, other duplicates have been found at K, L, MO, and P by the authors.

Mussaenda setosa is characterized by its long, slender, greenish white, strictly hirsute on the upper half, entirely glabrous in the lower half corolla tubes after anthesis. It is the only species observed wherein the stamens extend to the basal one fourth of the corolla in long-styled flower morphs. Jayaweera (1964) saw only one specimen of this species, which is the lectotype (long-styled flower morph). He suggested that *M. setosa* is similar to *M. palawanensis*, which are both endemic to Palawan. Recent collections of *M. setosa* (including the short-styled flower morphs) revealed more distinct characters that are completely divergent from *M. palawanensis*. Based on vegetative characters, *M. setosa* is rather similar to *M. albiflora* in its densely hirsute young twigs, in the

length and indumentum of leaf petioles and stipules, and more obviously in the size, shape, texture, and indumentum of the leaves. However, they differ in flower morphology including the color of the corolla lobes. *Mussaenda setosa* and *M. liedae*, both endemic to Palawan, are the only Philippine species with all or only globular trichomes inside the corolla tube of long-styled flower morphs.

Additional specimens examined. PHILIPPINES. **Palawan:** Taytay, Ibangley, $10^{\circ}20'N$, $119^{\circ}20'E$, Alejandro 86 (L, UBT, Univ. Santo Tomas Hb.), 87 (NY, PNH, UBT, US); Ibangley Brookside Hill, Pagdanan Range, $10^{\circ}45'N$, $119^{\circ}33'E$, Ridsdale 156781 (L, PNH).

22. *Mussaenda ustii* Alejandro, Bot. J. Linn. Soc. 158: 88–90, fig. 1. 2008. TYPE: Philippines. Aklan: Panay Island, Nabas, Mt. Laserna, $11^{\circ}49'N$, $122^{\circ}05'E$, 28 Oct. 2002, G. J. D. Alejandro & J. C. Castro 28 (holotype, L!; isotypes, UBT! [barcode] 0002959, Univ. Santo Tomas Hb!).

Shrubs or small trees, 2–6 m tall; young twigs green, sparsely to densely hirsute, the trichomes more than 12-celled, white to brown; older branches with few to many lenticels, reddish or grayish brown, glabrous or with few scattered trichomes. Leaf blades elliptic or ovate-elliptic, or rarely obovate, $7\text{--}20 \times 4\text{--}8$ cm, membranaceous, sparsely pubescent above, sparsely or densely pubescent, especially on midrib and veins underneath; margins ciliate; apex acuminate or subcaudate, not conduplicate; base cuneate, or long attenuate; secondary veins in 9 to 12 pairs, prominent above; petioles 0.4–1.5 cm long, densely hirsute. Stipules ovate to triangular, $7\text{--}11 \times 5\text{--}8$ mm at the base, persistent or deciduous, abaxially with dense indument, adaxially with sparse indument only at the base; apex bifid \pm half of length, the lobes slightly diverging or not; colleters numerous, in groups of 2 at the base. Inflorescences spreading or congested, sparsely or densely hirsute; bracts numerous, lanceolate, entire or trilobed, $4\text{--}9 \times 1\text{--}3$ mm, densely pubescent underneath, glabrous above. Flowers odorless; pedicels 2–7 mm, with sparsely appressed trichomes; calyx tubes cup-shaped to shortly tubular, 3–4 mm, sparsely or densely hirsute; calyx lobes lanceolate or subulate, not recurved, $3.5\text{--}8 \times 1\text{--}1.5$ mm, hirsute outside, glabrous inside, occasionally with a single calycophyll; colleters as 1 or 2 pairs per lobe, in sinuses between calyx lobes; calycophylls elliptic or ovate, 5-nerved, $6\text{--}12.5 \times 4\text{--}7.5$ cm, white,

sparsely pubescent on the nerves of both sides, margins ciliate, apex acuminate, base cuneate or attenuate, stalks 1–2.5 cm, densely hirsute; corolla buds pilose or rarely hirsute, remaining pilose all over or becoming pilose only on the upper half and with few scattered trichomes below in open flowers; corolla tubes cylindrical, forming a distinctly swollen part around anthers, 2.5–3.8 cm, cream or yellowish white, with tuft of trichomes surrounding the opening; short-styled flower morphs with densely long, unstriated, ribbon-like trichomes to base of anthers from the top; long-styled flower morphs with dense, short, striated, ribbon-like trichomes to the short filaments from the top; corolla lobes lanceolate to ovate, $7\text{--}13 \times 3\text{--}6$ mm, recurved, yellow with white margins, abaxially pilose, adaxially papillate; apex not recurved, with 1-mm filiform apical appendages; stamens inserted to the distal 1/4 in short-styled flower morphs, around middle in long-styled flower morphs, filaments glabrous, anthers linear, 4.5–6 mm in short-styled flower morphs, 4–4.5 mm in long-styled flower morphs, glabrous, apex acute; pollen diameter to 16 μm , apertures 4, rarely 3; ovary $3\text{--}4 \times 1.5\text{--}2.5$ mm, style 3–5 mm in short-styled flower morphs, 18–20 mm in long-styled flower morphs, stigma smooth, 1.5–2.5 mm in short-styled flower morphs, 6–8 mm in long-styled flower morphs, recurved, semi-exserted to distinctly exserted in long-styled flower morphs. Fruits globose or ellipsoid, $1\text{--}2.4 \times 1\text{--}1.1$ cm, with dense warts, without vertical ridges, green, calyces deciduous, glabrous or sparsely pubescent; mesocarp 0.8–1 mm thick; pedicels 3–6 mm, sparsely pubescent; seeds $0.4\text{--}0.75 \times 0.35\text{--}0.65$ mm; exotesta cells with 3 to 8 pores on the inner tangential walls, tuberculate thickenings slightly prominent.

Local names. Agboy (BisPn); Buyon (Bis) according to Alejandro (pers. obs.).

Phenology. *Mussaenda ustii* has been observed to flower from September to February, and fruit from October to December.

Distribution and habitat. *Mussaenda ustii* is endemic to Panay Island and is known from low-altitude humid evergreen forests, on stream banks, on roadsides, in open areas, or in partly shaded sites, occasionally growing with ferns or with *Imperata cylindrica* (L.) P. Beauv. (Poaceae), on clay-loam soils. It has been collected at altitudes ranging from 50 to 450 m.s.m.

Discussion. This species is easily distinguished by its long flower pedicels to 7 mm, by the yellow corolla lobes with white margins (forming a star pattern), and by the recurved and exserted stigma lobes in long-styled flower morphs. *Mussaenda ustii* resembles *M. anisophylla* and *M. albiflora* in the morphology and indumentum of vegetative parts but totally differs in its reproductive morphology.

Additional specimens examined. PHILIPPINES. **Aklan:** Panay, Nabas, Mt. Laserna, $11^{\circ}49'N$, $122^{\circ}05'E$, *Alejandro* 26 (NY), 27 (*Univ. Santo Tomas Hb.*), 32 (UBT, US), 40 (PNH, *Univ. Santo Tomas Hb.*); Ibajay, Brgy. Tagbaya, Mt. Bubog, $11^{\circ}49'N$, $122^{\circ}09'E$, *Alejandro* 38 (NY), 39 (*Univ. Santo Tomas Hb.*, WAG); Buruanga, Brgy. Tigum, Mt. Mangamura, $11^{\circ}50'N$, $121^{\circ}53'E$, *Alejandro* 44 (L, UBT), 47 (*Univ. Santo Tomas Hb.*), 48 (BR, *Univ. Santo Tomas Hb.*), 52 (PNH, *Univ. Santo Tomas Hb.*), 53 (BR), 54 (*Univ. Santo Tomas Hb.*, US), 56 (NY, US, WAG).

23. *Mussaenda vidalii* Elmer, *Leafl. Philipp. Bot.* 3: 993–994. 1911. TYPE: Philippines. Davao del Sur: Todaya, Mt. Apo, $07^{\circ}00'N$, $125^{\circ}16'E$, Aug. 1909, A. D. E. Elmer 11309 (lectotype, first designated by Jayaweera [1964: 139], GH, noting isotypes at A, NY, US; subsequent lectotype [cf. Art. 9.17], designated here, GH [barcode] 00096205 digital image!; isolectotypes, A [bc] 00096207!, E [bc] 00502301 digital image!, GH [bc] 00096206 digital image!, K [bc] K000740971 digital image!, MO [bc] 000716930 digital image!, NY [bc] 00132318!, U [bc] 0227259 digital image!, US [bc] 000917576!). Figure 23.

Shrubs or scandent shrubs, 3–5 m tall; young twigs green, sparsely to densely hirsute, the trichomes more than 12-celled, brown; older branches with few lenticels, grayish brown, glabrous or with few scattered trichomes. Leaf blades ovate, or ovate-elliptic, $9\text{--}27 \times 4.3\text{--}15.2$ cm, membranaceous to subcoriaceous, sparsely to densely hirsute on both sides, especially on midrib and veins underneath; margins ciliate; apex acute to acuminate, not conduplicate; base broadly obtuse, or cuneate; secondary veins in 6 to 11 pairs, prominulous above; petioles 1.5–5 cm long, densely hirsute. Stipules triangular, $5\text{--}10.5 \times 5.5\text{--}9$ mm at the base, persistent or deciduous, abaxially hirsute, adaxially sparsely hirsute only at the base and apex; apex bifid 1/4 to \pm half of length, the lobes slightly diverging; colleters few to numerous, in continuous rows or in groups of 2 at the base. Inflorescences spreading or congested, sparsely to densely hirsute, bracts few, linear-lanceolate, entire or trilobed, $3\text{--}16 \times 1.5\text{--}3$ mm, densely pubescent underneath, glabrous or sparsely pubescent above. Flowers

odorless; pedicels 1–1.5 mm long, with densely appressed trichomes; calyx tubes cup-shaped to shortly tubular, 3–4 mm long, densely hirsute; calyx lobes lanceolate to ovate, not recurved, $4\text{--}10 \times 1\text{--}3$ mm, pubescent on both sides, occasionally with a single calycophyll; colleters as 2 to 4 pairs per lobe, in sinuses between calyx lobes; calycophylls broadly ovate, 5-nerved, $5\text{--}10 \times 2.5\text{--}8.5$ cm, white, sparsely pubescent on the nerves of both sides; margins ciliate; apex acuminate; base cuneate to obtuse; stalks 1.4–2 cm long, densely hirsute; corolla buds densely hirsute, remaining hirsute all over or only on the upper half and with few scattered trichomes below in open flowers; corolla tubes infundibular, swollen part around anthers indistinct, 2.2–3 cm long, yellowish green, without tuft of trichomes surrounding the opening; short-styled flower morphs with densely long, unstriated, ribbon-like trichomes internally to the base of anthers from the top; long-styled flower morphs with sparsely short, striated, ribbon-like trichomes internally to the short filaments from the top; corolla lobes orbicular or broadly elliptic, $4\text{--}5 \times 4\text{--}6$ mm, orange to yellow, abaxially hirsute, adaxially papillate; apex not recurved, without filiform apical appendages. Stamens inserted to distal 1/4 in short-styled flower morphs, distal 1/4 to around the middle in long-styled flower morphs; filaments glabrous; anthers linear, 5–6.2 mm long in short-styled flower morphs, 4–4.5 mm long in long-styled flower morphs, glabrous, apex acute; pollen diameter to $16.65\text{ }\mu\text{m}$, apertures 4; ovary $3.5\text{--}5.5 \times 1.5\text{--}2$ mm; style 2.5 mm long in short-styled flower morphs, 17–25 mm long in long-styled flower morphs; stigma 2–2.5 mm long in short-styled flower morphs, 6–8 mm long in long-styled flower morphs, smooth, not recurved and included or semi-exserted in long-styled flower morphs. Fruits ellipsoid, $1.5\text{--}2.2 \times 1\text{--}1.4$ cm, with sparse to dense warts, without vertical ridges, green, calyces \pm persistent, densely hirsute; mesocarp 0.5–0.8 mm thick; pedicels 4–6 mm long, densely hirsute; seeds $0.53\text{--}0.73 \times 0.4\text{--}0.75$ mm; exotesta cells with 3 to 8 pores on the inner tangential walls, tuberculate thickenings slightly prominent.

Local names. Agat (Ifg); Ananayop, Anan-yop (BisSL); Botay (Bgb); Bukang-bukang (Bkd); Buyon (Bis); Salomayag (Mbo), according to Alejandro (pers. obs).

Phenology. *Mussaenda vidalii* was observed to flower from February to August, and fruit in March to May.

Distribution and habitat. *Mussaenda vidalii* has been collected in the provinces of Ifugao (Luzon), Biliran and Samar (Visayas), and mostly in Agusan del Norte, Bukidnon, Davao del Sur, and Lanao del Sur (Mindanao). This species is known from low- to high-altitude secondary forests, on coastal scrubs, on stream banks, on clay or sandy soils, at altitudes from 100 to 2000 m.s.m.

Discussion. Jayaweera (1964) designated a lectotype for *Mussaenda vidalii* at GH, but there are two duplicates of the original gathering (*Elmer 11309*) at GH. Applying Article 9.17 (McNeill et al., 2012), the GH material is further discriminated in subsequent or second step lectotypification, with GH (barcode) 00096205 specified as the lectotype and the second GH sheet as isoelectotype. This corresponds with Jayaweera's determination labels on the two GH sheets. Additional isoelectotypes were found at E, K, MO, and U. For purposes of citation, the more recent author of the second step typification is the one to be cited.

The type specimen of *Mussaenda vidalii* was described as a scandent shrub, but most of the herbarium collections for this species represent erect shrubs or small trees. *Mussaenda vidalii* is remarkable for its densely ferruginous vegetative and reproductive parts, by its large leaf blades to $9\text{--}27 \times 4.3\text{--}15.2$ cm, broadly ovate to elliptic in shape, by the petioles to 1.5–5 cm, by the stipules broad-based, adaxially hirsute only at the base and apex, by the calyx lobes ovate, broader than the long corolla lobes to $4\text{--}5 \times 5\text{--}6$ cm, and by the large fruits that are densely hirsute fruits. Variability within *M. vidalii* is restricted to the habit, bract sizes, and by the size and shape of sepals, petals, and fruits. *Mussaenda anisophylla* is obviously the nearest relative of *M. vidalii* due to its densely hirsute corolla buds, by the length of petioles to 1.5–5 cm, by the length of corolla tubes to 3 cm, and with a maximum diameter of pollen to $16.65\text{ }\mu\text{m}$, also the maximum diameter for pollen in *M. vidalii*. The two species differ in the shape of calyx lobes, and shape and indumentum of stipules. *Mussaenda vidalii* has lanceolate or ovate calyx lobes that are triangular and adaxially hirsute only at the base and apex of stipules, whereas *M. anisophylla* is characterized by linear calyx lobes that are ovate and adaxially with even coverage of the hirsute indument of the stipules.

Additional specimens examined. PHILIPPINES. **Agusan del Norte:** Tungao, logging camp, $08^{\circ}47'\text{N}$, $125^{\circ}35'\text{E}$, *Caballes 98444* (PNH), *Mabesa & Escasino 98452* (PNH); Butuan, Tungao So., San Mateo Bo., $08^{\circ}57'\text{N}$, $125^{\circ}34'\text{E}$, *Mendoza 42076* (PNH), *42373* (PNH); Asiga river,

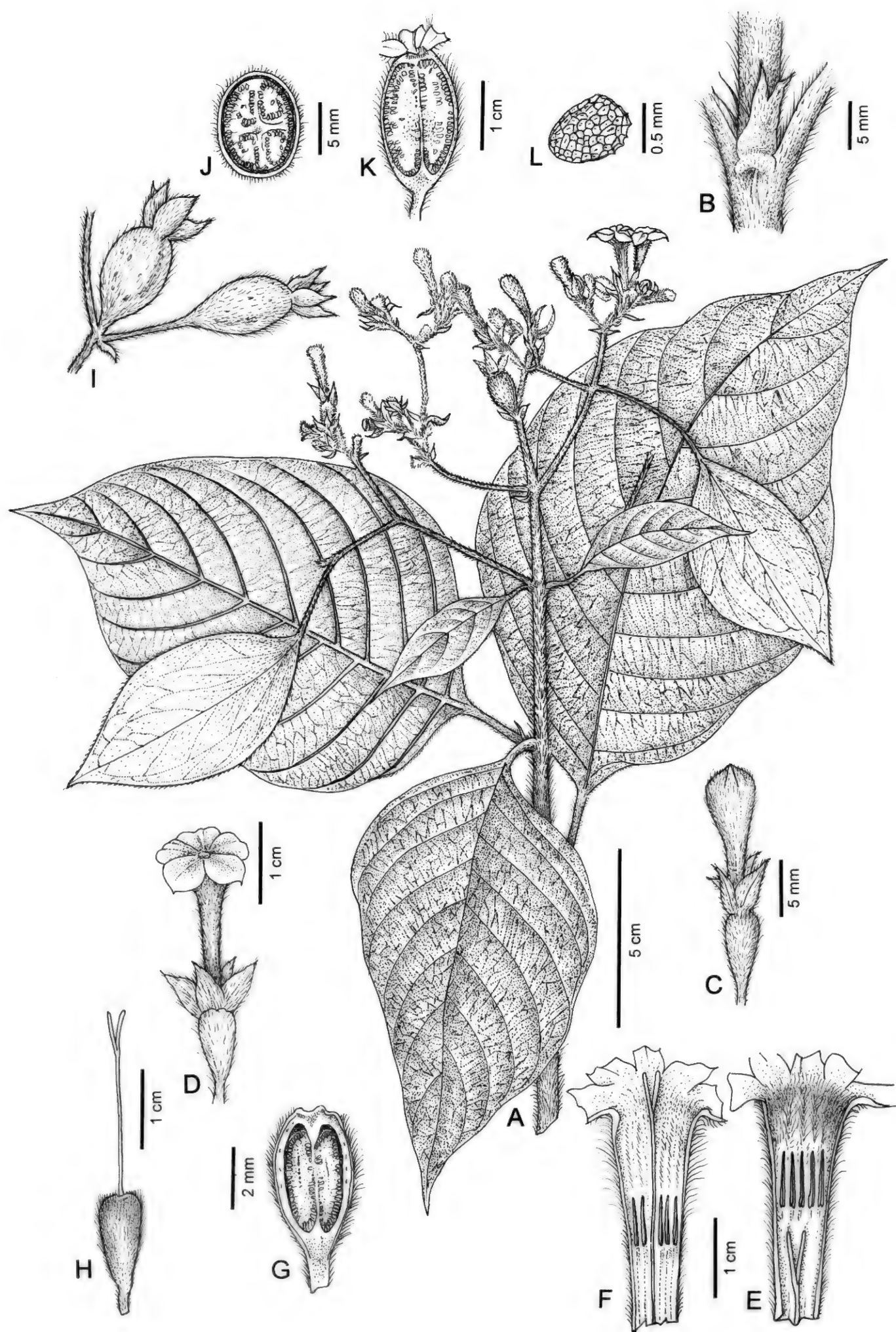


Figure 23. *Mussaenda vidalii* Elmer. —A. Flowering branch, with one fruit evident at center. —B. Portion of stem with stipule. —C. Flower bud. —D. Open anthesal flower. —E. Short-styled flower morph, corolla tube dissected open in longitudinal section. —F. Long-styled flower morph, corolla tube dissected open in longitudinal section. —G. Longitudinal section through ovary. —H. Calyx, style, and stigma of long-styled flower morph, with the corolla and calyx lobes removed. —I. Two fruits. J–K. Fruit sections showing seed attachments on placentas, in cross and longitudinal sections, respectively. —L. Seed. A–D, F–H are taken from *Sulit* 14366 (PNH); E, from *Sulit* 21530 (PNH); I–L, from *Edaño* 11926 (L).

09°26'N, 125°54'E, *Ramos & Convozar* 83671 (A). **Biliran:** Biliran Island, Mt. Suirio, N slope, 11°30'N, 124°29'E, *Sulit* 21530 (PNH). **Bukidnon:** Pintaoranan, 08°08'N, 125°00'E, *Anonuevo* 13516 (A, PNH); Damulog, Tangculan & vic., 07°48'N, 124°54'E, *Ramos & Edaño* 39050 (A). **Davao del Sur:** Mindanao region, Todaya, Mt. Apo, 07°00'N, 125°16'E, *Clemens* 15729 (NY). **Ifugao:** Banaue, Bayninan, 17°10'N, 120°45'E, *Conklin & Buwaya* 79609 (A, PNH). **Lanao del Sur:** Dansalan vic. (now Marawi City), 08°00'N, 124°18'E, *Zwickey* 519 (A). **Leyte:** Ormoc, Lake Danao, 11°00'N, 124°36'E, *Edaño* 11926 (L, PNH), Antilao River, 11°02'N, 124°32'E, *Edaño* 11873 (L, PNH), *Wenzel* 667 (A, MO). **Samar:** Catubig River, 12°23'N, 125°03'E, *Ramos* 24485 (A, US); Loquilocon Wright, 11°47'N, 125°06'E, *Sulit* 6098 (A, PNH); Concord, Bagacay, 11°35'N, 124°49'E, *Sulit* 6280 (PNH); Catarman, Lope de Vega, Mt. Cansayao, 12°29'N, 124°37'E, *Sulit* 14366 (A, PNH, US).

24. *Mussaenda viridiflora* Alejandro, Bot. J. Linn. Soc. 158: 90–91, fig. 2. 2008. TYPE: Philippines. Aklan: Panay Island, Buruanga, Brgy. Tigum, Mt. Mangamura, 11°50'N, 121°53'E, 30 Oct. 2002, *G. J. D. Alejandro & J. C. Castro* 49 (holotype, *Univ. Santo Tomas Hb.*!; isotype, L!).

Shrubs, 1.5–2 m tall; young twigs green, sparsely hirsute, the trichomes more than 12-celled, brown; older branches with few to many lenticels, reddish brown, glabrous or with few scattered trichomes. Leaf blades elliptic, 9.5–19.5 × 4.2–7.3 cm, membranaceous, sparsely pubescent, especially on the midrib and veins of both sides; margins ciliate; apex acuminate, or subcaudate, not conduplicate; base cuneate or attenuate; secondary veins in 8 to 12 pairs, prominulous above; petioles 0.4–3 cm long, sparsely to densely hirsute. Stipules ovate to triangular, 8–10 × 5–7 mm at the base, deciduous, with dense indument on both sides; apex bifid ± half of length, the lobes not diverging; colleters numerous, in groups of 2 at the base. Inflorescences spreading or congested, sparsely hirsute; bracts few, lanceolate, entire or trilobed, 3–8 × 2–3.5 mm, densely pubescent underneath, sparsely pubescent above. Flowers sweet-scented; pedicels 1–1.5 mm long, with sparsely appressed trichomes; calyx tubes cup-shaped to shortly tubular, 3–3.5 mm long, puberulous; calyx lobes lanceolate or subulate, strongly recurved, 3–4 × 1–1.5 mm, pubescent on both sides, occasionally with a single calycophyll; colleters as 1 pair per lobe (sometimes absent), in sinuses between calyx lobes; calycophylls ovate, 5-nerved, 7.9–9 × 4–5 cm, white, glabrous or puberulous on the nerves of both sides; margins ciliate; apex acuminate; base obtuse; stalks 2.3–2.8 cm long, densely pubescent; corolla buds densely pubescent, becoming sparsely pubescent in open flowers; corolla tubes cylindrical, forming a dis-

tinctly swollen part around anthers, 3–3.5 cm long, greenish white, with tuft of trichomes surrounding the opening; short-styled flower morphs with densely long, unstriated, ribbon-like trichomes to the base of anthers from the top; long-styled flower morphs not seen; corolla lobes ovate, 8–10 × 3–4 mm, white, green-tinged at the median ridges and bases, abaxially pubescent, adaxially papillate; apex recurved, with 1.5–2 mm long filiform apical appendages. Stamens inserted to distal 1/4 in short-styled flower morphs; filaments glabrous; anthers linear, 5–5.5 mm long in short-styled flower morphs, glabrous, apex acute; pollen diameter to 15.75 µm, apertures 4; ovary 3–4 × 1.5–2 mm; style 3.5–4 mm long in short-styled flower morphs; stigma smooth, 2–2.5 mm long in short-styled flower morphs. Fruits not seen.

Local name. Agboy (BisPn); Buyon (Bis), according to Alejandro (pers. obs.).

Phenology. *Mussaenda viridiflora* has been collected in flower from October to November, and is probably fruiting in January to March.

Distribution and habitat. *Mussaenda viridiflora* is endemic to Panay Island. It has been collected at lower altitudes of Mount Mangamura, near the road going to Ignito Cave, on open areas with rich herb layers, on clay-loam soils, and at altitudes of 300 m.s.m.

Discussion. This species is only known from the type collection. *Mussaenda viridiflora* is characterized by its sweet-scented flowers, white and green-tinged at the base, by the median ridges of corolla lobes, and by its strongly reflexed calyx lobes similar to the African *M. arcuata*, which is a feature not observed in other Philippine *Mussaenda* species. *Mussaenda viridiflora* resembles *M. albiflora* in its vegetative parts and white corolla lobes. However, *M. viridiflora* has less indumentum on vegetative structures, and its white corolla lobes are green-tinged on the median ridges and lobe bases. Based on reproductive morphology, *M. viridiflora* is more similar to *M. philippica* var. *philippica* and *M. pinatubensis* due to the shape of corolla lobes and indumentum of flowers.

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Appendix 1. List of *Mussaenda* species and varieties included in this study. Numbers indicate their position within the taxonomic treatment.

1. *Mussaenda acuminatissima* Merr.
2. *Mussaenda albiflora* Merr.
3. *Mussaenda anisophylla* S. Vidal
4. *Mussaenda attenuifolia* Elmer
5. *Mussaenda benguetensis* Elmer
6. *Mussaenda chlorantha* Merr.
7. *Mussaenda grandibracteata* Alejandro
8. *Mussaenda grandifolia* Elmer
9. *Mussaenda lanata* C. B. Rob.
10. *Mussaenda liedeeae* Alejandro
11. *Mussaenda macrophylla* Wall.
- 11a. *Mussaenda macrophylla* var. *brevipilosa* Jayaw.
- 11b. *Mussaenda macrophylla* var. *grandisepala* (Jayaw.) Alejandro
- 11c. *Mussaenda macrophylla* Wall. var. *macrophylla*
12. *Mussaenda magallanensis* Elmer
13. *Mussaenda milleri* Elmer ex Alejandro
14. *Mussaenda multibracteata* Merr.
15. *Mussaenda nervosa* Elmer
16. *Mussaenda palawanensis* Merr.
17. *Mussaenda philippica* A. Rich.
- 17a. *Mussaenda philippica* var. *aurorae* Sulit
- 17b. *Mussaenda philippica* A. Rich var. *philippica*
- 17c. *Mussaenda philippica* var. *pubescens* Alejandro
18. *Mussaenda philippinensis* Merr.
19. *Mussaenda pinatubensis* Elmer
20. *Mussaenda scandens* Elmer
21. *Mussaenda setosa* Merr.
22. *Mussaenda ustii* Alejandro
23. *Mussaenda vidalii* Elmer
24. *Mussaenda viridiflora* Alejandro

Appendix 2. Index to numbered collections. Examined specimens are listed alphabetically according to the principal collector, followed by the collection number. The numbers in parentheses correspond to the number of species and varieties in Appendix 1 and in the taxonomic treatments. Asterisks indicate type collections. This index includes all specimens examined by the authors, not only those mentioned in the taxonomic treatments.

Adduru, M. 218 (17b); *Ahern*, G. P. 339 (17b), 818 (17b); *Alcasid & Oane* 39863 (17b); *Alejandro*, G. J. D. 1 (19), 3 (12), 4 (17b), 5 (12), 7 (17b), 8 (17b), 9 (17a), 10 (17b), 11 (17b), 12 (17b), 13 (7), 15 (7), 16 (7), 17 (7), 19 (17b), 20 (2), 21 (17b), 22 (17b), 23 (17b), 24 (17b), 25 (17b), 26 (22), 27 (22), 29 (2), 30 (2), 31 (2), 32 (22), 33 (17b), 34 (17b), 35 (17b), 36 (2), 37 (2), 38 (22), 39 (22), 40 (22), 41 (17b), 43 (2), 44 (22), 45 (17b), 46 (2), 47 (22), 48 (22), 50 (2), 51 (2), 52 (22), 53 (22), 54 (22), 55 (17b), 56 (22), 57 (17b), 58 (17b), 59 (17b), 60 (1), 61 (17b), 65 (3), 63a (14), 63b (14), 64 (17b), 66 (16), 67 (16), 68 (16), 70 (17b), 72 (16), 73 (16), 74 (17b), 75 (16), 76 (16), 77 (16), 78 (16), 79 (17b), 80 (17b), 82 (16), 83 (16), 84 (16), 85 (17b), 86 (21), 87 (21), 88 (10), 89* (10), 90 (10), 91 (17b), 92 (20), 93 (17b), 94 (17b), 95 (15), 96 (17b), 97 (17b), 98 (19), 99 (17b), 100 (17b), 101 (9), 102 (17b), 103 (17b), 105 (17b), 106 (17b), 107 (5), 108 (5), 109 (6), 110 (5), 111 (5), 104 (17b), 10049 (15), 10164 (17b); *Alejandro*, G. J. D. & *Castro*, J. C. 14* (7), 28* (22), 49* (24); *Allen*, M. S. 150272 (17b); *Anonuevo*, P. 13516 (23); *A. N. U.* 1564 (17c).

Banlunan, G. 72607 (3); *Banzon*, R. 128204 (17b); *Bartlett*, H. 13459 (3), 14653 (17b), 15545 (18); *Bermejor*, J. 182 (17b), 350 (17b); *Bhargava*, N. 1757 (11c); *Bhern*, G. P. 802 (17b); *Bolster*, F. H. 136 (17b); *Borden*, T. E. 1220 (17b); *Borromeo*, H. 25602 (3); *Bourell*, M. 2244 (16); *Brenner*, L. G. 2584 (17b); *Britton*, B. B. 120 (12); *Burley*, J. S. 95 (17b), 147 (12).

Caballes, R. A. 98444 (23); *Canicosa*, E. 9730 (3), 9765 (17b); *Castro*, A. 5782 (17b), 5810 (17b), 5853 (17b); *Celestino*, M. 7819 (3), 7879 (6); *Cenabre*, A. L. 29149 (17b); *Chang*, C. E. 2754 (11c); *Clemens*, M. S. 15729 (23), 17011 (14), 17249 (9), 51845 (5); *Conese*, E. 15797 (17b); *Conklin & Buwaya* 79609 (23), 80640 (5); *Conklin*, H. C. & *del Rosario* 72628 (3), 72703 (5); *Convocar*, P. 2820 (14), 2945 (17b); *Copeland*, E. B. 355 (20); *Cordero*, P. & *Espiritu*, R. 91572 (16); *Cuming* 918* (3), 1368 (17b); *Curran*, H. M. 4517 (17b), 10535 (17b), 17358* (2).

Danao, F. 19907 (17b); *Deguchi*, K. et al. 6303 (17b); *del Rosario*, R. 79959 (11a); *del Rosario & Corsero* 96180 (3); *Delprete*, P. 6458 (17b); *Demetrio & Mendoza* 36232 (17b); *DeVore & Hoover* 172 (17b); *Dias*, F. 29885 (2).

Ebalo, L. E. 193 (18), 718 (17b), 67441 (16); *Ebalo*, L. E. & *Conklin*, H. C. 1227 (16); *Edaño*, G. E. 114 (3), 244 (16), 373 (3), 1312 (17b), 1527 (17b), 3290 (3), 3500 (3), 11074 (17b), 11384 (17c), 11873 (23), 11926 (23), 15450 (17b), 19875 (18), 21782 (17c), 21809 (17c), 37163 (17b), 37164 (17b), 40230 (14), 46114 (12), 46220 (17b), 75879 (17b), 76425 (14), 79448 (11a); *Edaño*, G. E. & *Gutierrez*, H. 37744 (17b), 38555 (17b); *Edaño*, G. E. & *Ramos*, M. 40589 (3); *Elmer*, A. D. E 5935* (5), 6195 (9), 6318 (6), 6381 (6), 6536 (5), 6673 (17b), 7045 (17b), 8134 (17b), 8431 (5), 8976 (9), 9154 (3), 9535 (5), 9966 (6), 10121 (17b), 10510* (15), 11291* (20), 11309* (23), 12451* (12), 12792 (17b), 13301 (17b), 13304* (4), 14388 (17b), 17481 (3), 17670 (17b), 21940 (6), 21978* (19); *Escritor*, L. 21192 (17b); *Espiritu*, R. 91473 (16).

Fenix, E. 3770* (11a), 15531* (16), 26030 (17b), 29851 (3); *Fosberg*, F. R. 35017 (17b), 35018 (17a); *Fox*, R. B. 4586 (17b), 9021 (17b), 13354 (16); *Foxworthy*, F. W. 605 (17b), 691 (17b), *Frake*, C. O. 20332 (17b), 36058 (17b) 38115 (17b); *Frohne*, G. M. 35140 (17b).

Gammill, J. A. 261 (17b); *Garcia, F. C.* 34977 (5); *Gatchalian, F.* 15493 (17b); *Gutierrez, H. G.* 77986 (17b); *Gutierrez, Y. & Reynoso* 108958 (17b).
Hallier, H. s.n., s.d. (17b).
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Jocano, F. L. 40696 (17b).
Kanehira, R. 2497 (17b); *Kondo, Y. & Edaño, G.* 36685 (16).
Loher, A. 1524 (9).
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Taleon, A. T. 33828 (17b); *Topping, D. L.* 64 (5).
Valbuena, R. & Lopez, F. 91899 (5); *Vanoverbergh, F. M.* 190 (6); *Varadarajan, G. S.* 1531 (2); *Velasco, V.* 26650 (11a), 24852 (17b); *Velasquez, G. T. s. n.* [1 Dec. 1953] (17b); *Vidal* 389 (17b), 801 (3), 1457 (17b).
Walker, E. H. 7456 (17a), 7501 (5); *Wallich* 6225* (11c); *Wenzel, C. A.* 57 (17b), 179 (17b), 442 (12), 667 (23), 3354 (20); *Whitford, H. N.* 388 (17b), 524 (17b); *Williams, R. S.* 127 (17b), 1006 (5), 1011 (9), 1588 (9), 2854 (17b).
Zwickey, A. L. 34 (17b), 519 (23).

ORIGINS AND RELATIONSHIPS OF THE MIXED MESOPHYTIC FOREST OF OREGON–IDAHO, CHINA, AND KENTUCKY: REVIEW AND SYNTHESIS¹

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ABSTRACT

The Arcto-Tertiary Geoflora concept of Ralph Chaney, that the Mixed Mesophytic Forest of eastern Asia and eastern North America are relicts of a Northern Hemisphere high-latitude circumglobal deciduous forest of the Late Cretaceous–Early Tertiary that migrated south to the temperate zone as an intact unit, was shown by Wolfe and others to be invalid. To explain the origin and development of these disjunct forests, Wolfe and Tiffney developed the boreotropical hypothesis. Accordingly, a paratropical (near-tropical) rainforest flora containing a mixture of tropical, paratropical, and temperate genera developed at several places in the middle latitudes of the Northern Hemisphere in the Eocene and spread around the globe via the Bering and North Atlantic land bridges and shores of the Tethys Seaway. Further, the Mixed Mesophytic Forest of eastern Asia and eastern North America developed independently after disruption of the boreotropical flora by subsequent changes in climate and geography, thus accounting for differences in the flora and physiognomy of the present-day Mixed Mesophytic Forest in the two areas. The fruit and seed flora of the Middle Eocene Clarno Nut Beds of Oregon are representative of the boreotropical forest. In response to climatic cooling during the Eocene–Oligocene transition, this broad-leaved evergreen rainforest was replaced by a temperate broad-leaved deciduous (Mixed Mesophytic) forest, which remained present in the Pacific Northwest through most of the Miocene. The Early Oligocene Bridge Creek flora of Oregon, the Middle Miocene Succor Creek flora of eastern Oregon and adjacent Idaho, and the Middle Miocene Clarkia and Musselshell Creek floras of northern Idaho are good examples of the Mixed Mesophytic Forest. These Oligocene–Miocene fossil floras include important genera in the present-day Mixed Mesophytic Forest of eastern Asia and eastern North America, as well as those that today occur only in eastern Asia or only in eastern North America. Using Graham as the primary source of, and guide to, information on microfossil and megafossil plant paleoassemblages and paleoclimates in eastern North America, we chart the Late Cretaceous–Tertiary sequence of vegetation and climate for Kentucky. Further, we briefly review the palynofloral provinces in which Kentucky was situated during the Middle and Early Cretaceous. In contrast to the Mixed Mesophytic Forest flora (a component of the boreotropical forest) of the Middle Eocene Clarno Nut Beds, the Middle Eocene Claiborne flora of Tennessee and Kentucky represents a semideciduous tropical dry forest dominated by Leguminosae taxa that have strong phylogenetic and biogeographical relationships with the Old World and tropical South America. Apparently, this dry forest developed from a Paleocene–Early Eocene tropical rainforest following a decrease in amount and an increase in seasonality of rainfall. The Mixed Mesophytic Forest developed from this seasonally dry forest following the Eocene as a result of an increase in the amount of rainfall and a decrease in its seasonality. The hypothesis that closely related disjunct taxa between eastern Asia and eastern and western North America represent relicts of a circumglobal Mixed Mesophytic Forest in the Miocene is supported by fossil and molecular phylogenetic data.

Key words: Arcto-Tertiary Geoflora concept, biogeography, boreotropical hypothesis, China, Mixed Mesophytic Forest, North America.

Ever since Linnaeus (Graham, 1966, 1972; Boufford & Spongberg, 1983; Wen, 1999), botanists have known that there are many similarities at the generic level between the deciduous forest floras of eastern North America and those of eastern Asia (Gray, 1840, 1846, 1859, 1878; Fernald, 1931; Li, 1952, 1972; Graham, 1972; Wood, 1972; Boufford & Spongberg, 1983; Wu, 1983; Boufford, 1992; Hong, 1993; Xiang et al., 1998, 2000; Manchester, 1999; Qian, 1999, 2002; Wen, 1999; Guo & Ricklefs, 2000). Less well known, however, is that there is a high similarity between the Middle to Late Tertiary Mixed Mesophytic Forest of western North America

and the modern Mixed Mesophytic Forest of eastern Asia (China, Japan, Korea) and eastern North America (Meyer & Manchester, 1997). The primary purpose of this review is to discuss the origins of, and the floristic and physiognomic relationships between, the Tertiary Mixed Mesophytic Forest of Oregon–Idaho and the present-day Mixed Mesophytic Forest of China and Kentucky.

ARCTO-TERTIARY GEOFLORA CONCEPT

According to the Arcto-Tertiary Geoflora concept (e.g., Chaney, 1940, 1944, 1947, 1948, 1959;

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Axelrod, 1966, 1983; also see Gray, 1878), the forests of eastern North America, eastern Asia, and western and central Europe are relicts of a temperate, broad-leaved deciduous forest (Arcto-Tertiary forest) of a particular floristic composition (Arcto-Tertiary Geoflora, *sensu* Chaney, 1959) that evolved (in association with some deciduous gymnosperms such as *Ginkgo* L. and *Metasequoia* Hu & W. C. Cheng) at high northern latitudes during the Late Cretaceous and Early Tertiary, moved southward across North America, Europe, and Asia, as the climate cooled, and became distributed across the Northern Hemisphere by the Miocene. In response to climatic cooling, this climax forest community migrated more or less intact to middle latitudes in the Oligocene.

According to Wolfe (1994: 224), “Chaney’s hypothesis differs little from that of Asa Gray (1878), and his usage of ‘arcto-tertiary’ differs little from that of Engler (1882), who first coined the term.” Some assumptions of Chaney’s hypothesis are as follows. A temperate climate predominated at northern latitudes, and thus vicariant patterns should be found only in temperate taxa, such as the disjuncts between eastern Asia and eastern North America. As such, the cool temperate climate precluded the migration of tropical taxa between the Old World and the New World. A Neotropical Tertiary Geoflora occurred south of the Arcto-Tertiary Geoflora, and the ultimate source of this tropical flora was South America. Land bridges (Beringian) between Eurasia and North America facilitated exchange (or interchange) of primarily temperate plants between these continents. Climate tolerance of fossil flora was the same as that of modern analogs, i.e., no change in tolerance through geological time. This temperate, broad-leaved deciduous forest (i.e., fossil assemblage) closely resembled the North American Eastern Deciduous Forest (many genera the same), and it was stable over a wide interval of time and space (tens of millions of years and thousands of kilometers). A detailed account of the history and philosophy of the Arcto-Tertiary Geoflora concept is given by Wolfe (1977; see also Graham, 1972; Lavin & Sousa S., 1995).

The major present-day Northern Hemisphere moist-temperate deciduous forest regions left over from fragmentation of this circumglobal forest are in eastern Asia, Europe, and eastern North America. Tree species richness differs considerably among these three regions, with richness greater in eastern Asia than in eastern North America and richness greater in eastern North America than in Europe (Latham & Ricklefs, 1993; Guo et al., 1998; Svenning, 2003). The Mixed Mesophytic Forest of Oregon–Idaho and of western North America in

general were extirpated by the Late Miocene by increasing summer-dry conditions caused by the rain shadow resulting from the rise of the Cascades and Coastal Ranges (Chaney, 1936, 1938a, 1938b, 1959; Wolfe, 1969, 1981; Graham, 1972; Axelrod & Schorn, 1994). This drying climate in western North America caused extinction of many taxa of the Mixed Mesophytic Forest in that region, which probably accounts, at least in part, for the considerably fewer disjunctions between eastern North America and western North America than between eastern North America and eastern Asia (Donoghue & Smith, 2004). Extirpation of mixed forest genera in the Oligocene (Meyer & Manchester, 1997) and Miocene (e.g., Smiley & Rember, 1981) has been supported by fossil data (see also Manchester, 1999).

Species richness of the forests of western and central Europe was reduced greatly in the Pliocene/Pleistocene via climatic cooling (Wolfe, 1997; Willis & McElwain, 2002; Svenning, 2003; Willis & Niklas, 2004). The classical explanation for tree species’ extinctions in Europe is that the east-west-trending mountains and the Mediterranean Sea prevented migration of plant taxa southward to warmer areas (Gray, 1878; Reid, 1935; Graham, 1972; Tiffney, 1985b; Milne & Abbott, 2002). However, according to Huntley (1993), evidence does not support east-west-trending mountains or the Mediterranean Sea being barriers to movement of tree taxa in Europe in the Quaternary. Instead, the greater extinction of trees at the generic level in Europe than in Asia and North America during the Quaternary was due to the greater reduction in forest area in Europe, i.e., “... limited areas available to such taxa on this continent during the glacial stages that have dominated the Quaternary” (Huntley, 1993: 170). Huntley suggests, however, that the increased species:genus ratio of the European tree taxa, due to speciation via long-term isolation during the Pliocene/Pleistocene in localized refugia in southern Europe, goes a long way in compensating for the greater extinction of tree genera in Europe than in Asia and North America. Further, according to Campbell (1982), certain woody plant genera, including *Alnus* Mill., *Corylus* L., *Pyrus* L., and *Taxus* L., are 100% to 1000% taller in Europe than they are in North America and they may be ecological substitutes for trees such as *Liriodendron* L., *Carya* Nutt. (*Tsuga* (Endl.) Carrière–*Thuja* L.), and *Diospyros* L., respectively, which are no longer extant in Europe. However, according to Huntley (1993: 170) the several genera that today are trees in Europe but low-growing trees/shrubs in eastern North America “...are too few in number to

compensate for these genera that have become extinct [in Europe].”

Svenning (2003) presented evidence that the differential extinctions in the cool temperate tree flora of Europe during the Pliocene/Pleistocene are related to differences in cold and drought tolerances among them. The cold tolerance of the genera in the Pliocene tree flora currently widespread in Europe is greater than that of the genera that went extinct during the Pliocene/Pleistocene or that survive today in Europe as relicts. Further, the relictual genera are more drought-tolerant than those that went extinct (Svenning, 2003). Svenning (2003) explained this differential survival of Pliocene tree genera as a deterministic ecological sorting process determined by generic evolutionary conservatism for tolerance to cold and drought. This suggests that tree genera that survived the Pliocene/Pleistocene extinctions in southern Europe did so either in cool, moist mid-elevation refuges (i.e., cold-tolerant genera) or in low-elevation, drought-prone refuges (i.e., drought-tolerant genera). Svenning and Skov (2007: 242) stated that numerous tree genera that today form an important component of the warm-temperature vegetation in eastern Asia and North America went extinct during the Plio-Pleistocene climatic changes because of “[t]he scarcity of warm moist glacial refugia....” Milne (2004) suggested that the survival of three or four lineages (four species) of *Rhododendron* L. subsect. *Pontica* (Tagg) Sleumer, a Tertiary relict group, in the southwestern Eurasian refugium during Quaternary glaciations can be attributed to their cold tolerance.

The traditional paradigm about the geographic location of European trees during the Pliocene–Pleistocene glaciations is that they were restricted to refugia (more accurately to refugia within refugia [Feliner, 2011]) in southern Europe, and in particular to the Balkan, Italian, and Iberian Peninsulas, where they grew in mid-elevation zones (ca. 500–800 m elevation) on mountains between lowland xeric steppe vegetation and high-elevation, tundra-like vegetation (Willis & McElwain, 2002; Willis & Niklas, 2004; Birks & Willis, 2008). However, current plant fossil material (pollen, plant macrofossils, and macroscopic charcoal) (Willis et al., 2000; Willis & Van Andel, 2004; Bhagwat & Willis, 2008; de Lafontaine et al., 2014a, 2014b), genetic evidence (de Lafontaine et al., 2013), and climatic niche modeling (Svenning et al., 2008) have documented the occurrence of at least 34 woody species of gymnosperms and angiosperms, most of them trees, that survived in cryptic refugia in tundra-type vegetation in central and eastern Europe, north of

the southern refugia during the latest glacial advance. Moreover, some taxa of angiosperm trees occurred in both northern and southern refugia.

BOREOTROPICAL HYPOTHESIS

To account for the floristic similarities between eastern North America, Europe, eastern Asia, and western North America, Wolfe and Tiffney proposed the boreotropical hypothesis, in recognition of the northern geography, near-tropical climate, and thermophilic affinities of the flora’s many component taxa (Wolfe, 1975, 1977; Tiffney, 1985a, 1985b). They derived this hypothesis on the basis of tropical taxa shared by the Eocene floras of Europe and North America and on the close taxonomic relationship of these floras to those present today in tropical Southeast Asia and, to some extent, Central America and the Greater Antilles (Lavin & Luckow, 1993). Thus, in contrast to the Arcto-Tertiary Geoflora concept, tropical climates and vegetation extended to northern latitudes during the Eocene (e.g., broad-leaved evergreen multistratal rainforest to 65°–70°N paleolatitudes in Alaska [Wolfe, 1985]), which allowed the exchange of tropical taxa via land bridges with the Old World tropical flora. According to this concept, a large number of modern taxa first appeared in the middle latitudes of the Northern Hemisphere in the Early Tertiary (latest Paleocene to Eocene) and spread via the Bering and North Atlantic land bridges and the shores of the Tethys Seaway. The Tethys Seaway was important for the spread of plants across Eurasia (see Wolfe & Leopold, 1967; Tiffney, 1985a, 1985b) and also for the spread of tropical, subtropical, and warm-temperate plants between Southeast Asia and the southeastern United States (Dilcher, 2000). Accordingly, the claim of the Arcto-Tertiary Geoflora concept that many lineages in this flora evolved in the Arctic during the Late Cretaceous is invalid. Thus, according to Spicer et al. (1987), the first appearance of a clade (woody angiosperms) present in Late Cretaceous–Early Tertiary floras is consistently later in Alaska than at middle latitudes. That is, lineages first appeared in low to middle latitudes and then in the Arctic (Spicer et al., 1987). The migration of angiosperms was poleward (Axelrod, 1959; Hickey & Doyle, 1977).

Wolfe (1994: 232) stated that “a few arcto-tertiary lineages (e.g., those of *Ginkgo* and *Metasequoia*) may even have histories as envisioned by Chaney (1938 [1938b]).” Thus Wolfe suggested that a few Arcto-Tertiary lineages may have diversified in montane environments at middle latitudes and then moved downslope as the climate cooled. Note, however, that Wolfe restricted his Arcto-Tertiary use in reference to

trees and shrubs of the Arctic Tertiary plant assemblages that now occur in eastern Asia and eastern North America. He did not embrace the Arcto-Tertiary Geoflora concept of Chaney. In fact, Wolfe stated, "... I consider the concept of an 'Arcto-Tertiary Geoflora' to be negated by the fossil record..." (1994: 232).

The boreotropical flora is postulated to have had a diffuse origin, i.e., appearing in several locations in the Northern Hemisphere. This flora had its origins from several separate sources and thus did not originate only in Southeast Asia (Tiffney, 1985b). Southeast Asia (Indomalayan area) is a refugium for the boreotropical flora, not its center of origin (Tiffney, 1985a; also see Schuster, 1972, 1976; Thorne, 1999). "Thus, much of the present Indomalayan flora can be thought of as a relict of this Paleogene boreotropical flora" (Wolfe, 1975: 269, 270). Further, this boreotropical flora was not homogeneous; it exhibited spatial and temporal change in taxonomic composition, and its taxa appeared in the fossil record at different times and had different ecologies (Tiffney, 1985a, 1985b). The boreotropical flora existed in a warm, equable (paratropical) climate with a mean annual temperature of 20°C–25°C and a low mean annual range of temperatures. This flora included a mixture of temperate, tropical, and paratropical genera, many of which were retained in/associated with the Mixed Mesophytic Forest of the Middle to Late Tertiary, e.g., *Acer* L., *Alangium* Lam., *Betula* L., *Calycocarpum* (Nutt. ex Torr. & A. Gray) Spach, *Carpinus* L., *Carya*, *Celtis* L., *Cercidiphyllum* Siebold & Zucc., *Cladrastis* Raf., *Cocculus* DC., *Fagus* L., *Gordonia* J. Ellis, *Halesia* J. Ellis ex L., *Hamamelis* L., *Hydrangea* L., *Juglans* L., *Liquidambar* L., *Liriodendron*, *Magnolia* L., *Nyssa* L., *Platanus* L., *Pterocarya* Kunth, *Quercus* L., *Tetracentron* Oliv., *Tilia* L., *Ulmus* L., and *Zelkova* Spach (Wolfe, 1977). These taxa still persist in the Mixed Mesophytic Forest of eastern Asia and/or eastern North America today.

Unlike the Arcto-Tertiary Geoflora concept, the boreotropical hypothesis views the Mixed Mesophytic Forest of eastern Asia and eastern North America as having developed *independently* (emphasis ours) after the geographical disruption of the boreotropical flora and not as lineal descendants (remnants, relicts) of a broad-leaved deciduous forest that evolved in high latitudes of the Northern Hemisphere and then migrated as an *intact unit* (emphasis ours) to middle latitudes during gradual climatic cooling during the Tertiary (i.e., Arcto-Tertiary Geoflora concept). According to Tiffney (1985b: 244), "Once the early Tertiary boreotropical flora had spread, it was

influenced and altered by subsequent geographic and climatic events, giving rise to the modern flora and vegetation of Eurasia and North America." Further, "... plants sharing a common distribution pattern in the modern day need not have attained this distribution in the same way at the same time" (Tiffney, 1985a: 84). Thus, the eastern Asian–eastern North American pattern in the extant flora of these two areas did not arise as a result of a single historical event.

According to Wolfe (1972, 1977, 1985), the vegetation of southern Alaska (ca. 70°N paleolatitude) in the Early Eocene was paratropical rainforest. This implies that the Bering land bridge may have served as a route for tropical evergreen taxa into North America from Asia in the Early Eocene (Tiffney, 2000). However, winter darkness may have presented a physiological barrier to evergreen taxa in crossing the Bridge (ca. 75°N paleolatitude, but see Royer et al., 2003; Beerling, 2007: chapter 6). Further, the evergreen floras studied by Wolfe were located on exotic terrains, in which case plants in this flora may have grown at more southern latitudes and were transported as fossils to their present localities (Tiffney, 2000; Tiffney & Manchester, 2001). Thus, while the North Atlantic land bridge seemed to have served as a migration route for tropical and subtropical plants during the Eocene (Tiffney, 2000; Tiffney & Manchester, 2001), the Bering land bridge may or may not have done so. Dilcher (2000: 18) postulated that the tropical/subtropical elements in the Eocene flora of the southeastern United States are not products of the northern routes proposed by the boreotropical hypothesis, but rather suggested that these high-latitude routes were too cold for the subtropical and tropical plants in the fossil flora of the southeastern United States, which "... must have been distributed under the warm climatic influence of the Tethys Sea."

MIDDLE EOCENE PARATROPICAL RAINFOREST OF OREGON

In North America, the fruit and seed flora of the Middle Eocene (ca. 44 million years ago [Ma]) Clarno Nut Beds of central Oregon is an excellent example of the boreotropical flora that was widespread across the Northern Hemisphere in the Eocene (Manchester, 1981, 1994). Today, the vegetation of this area of Oregon, which is in the rain shadow of the Cascade Mountains, is primarily shrub-steppe with scattered junipers at lower elevations and coniferous forests (*Abies* Mill., *Pinus* L., *Pseudotsuga* Carrière) at higher elevations (Franklin & Dyrness, 1988). Only five extant tree genera (*Celtis*, *Cornus* L., *Pinus*,

Table 1. Present geographical distribution (marked by x) of extant genera represented in the Middle Eocene Clarno Nut Beds flora (from Manchester, 1994), except *Sargentodoxa* Rehder & E. H. Wilson and *Torricellia* DC. (from Manchester, 1999).

Genus	Southeast Asia	Malesia	Western North America	Eastern North America	Central America	South America	Europe	Africa
<i>Actinidia</i> Lindl.	x	x						
<i>Alangium</i> Lam.	x	x						x
<i>Ampelocissus</i> Planch.	x	?			x			?
<i>Ampelopsis</i> Michx.	x	?		x				
<i>Anamirta</i> Colebr.	x	x						
<i>Aphananthe</i> Planch.	x	x			x			x
<i>Calycocarpum</i> Nutt. ex Torr. & A. Gray				x				
<i>Castanopsis</i> (D. Don) Spach	x	x	x					
<i>Celtis</i> L.	x	x	x	x	x	x	x	x
<i>Cleyera</i> Thunb.	x				x			
<i>Cornus</i> L.	x	x	x	x	x	x	x	x
<i>Decodon</i> J. F. Gmel.				x				
<i>Diploclisia</i> Miers	x	x						
<i>Emmenopterys</i> Oliv.	x	x						
<i>Ensete</i> Horan.	x	x						x
<i>Hydrangea</i> L.	x	x		x	x	x		
<i>Iodes</i> Blume	x	x						x
<i>Juglans</i> L.	x		x	x	x	x	x	
<i>Lindera</i> Thunb.	x			x				
<i>Magnolia</i> L.	x	x		x	x			
<i>Mastixia</i> Blume	x	x						
<i>Meliosma</i> Blume	x	x			x	x		
<i>Nyssa</i> L.	x	x		x	x			
<i>Parthenocissus</i> Planch.	x		x	x	x			
<i>Pinus</i> L.	x	x	x	x	x	x	x	x
<i>Platanus</i> L.	x		x	x	x		x	
<i>Prunus</i> L.	x		x	x	x	x	x	x
<i>Pyrenacantha</i> Hook.	x	x						x
<i>Quercus</i> L.	x	x	x	x	x	x	x	
<i>Rhus</i> L.	x	x	x	x	x	x	x	x
<i>Sabal</i> Adans.				x	x	x		
<i>Sabia</i> Colebr.	x	x						
<i>Sargentodoxa</i> Rehder & E. H. Wilson	x							
<i>Schisandra</i> Michx.	x	x		x				
<i>Symplocos</i> Jacq.	x	x	x	x	x	x		
<i>Tapiscia</i> Oliv.	x							
<i>Taxus</i> L.	x	x	x	x	x		x	
<i>Tinospora</i> Miers	x	x						x
<i>Torreya</i> Arn.	x	?	x	x				
<i>Torricellia</i> DC.	x							
<i>Trema</i> Lour.	x	x			x	x		x
<i>Vitis</i> L.	x		x	x	x		x	x
Totals	39	26	14	22	21	12	10	13

Quercus, and *Taxus*) in the Clarno Nut Beds flora are still native to Oregon; most are found in other geographic regions (Table 1). Thirty-nine (92.9%) of the 42 extant genera recorded from the fruit and seed flora of the Clarno Nut Beds are currently native to Southeast Asia, 26 (61.9%) to Malesia, and 22 (52.4%) to eastern North America (Manchester, 1994). Further, 28 of the 42 (66.7%) extant genera in the Clarno Nut Beds flora occur

in the Mixed Mesophytic Forest (sensu Wolfe, 1979) of eastern Asia. A smaller number also occurs in other types of deciduous forest in eastern Asia (Manchester, 1994). Thus, the boreotropical flora had a definite Indomalayan affinity, and the present distribution of this flora is in the Indomalayan area (Table 1; Wolfe, 1975). According to Manchester (1994: 27), “The close floristic similarity [of the Nut Beds flora]

with southeastern Asia and Malesia probably reflects the status of this area as a refugium for once-widespread thermophilic genera that could not withstand the effects of climatic cooling and glaciation at the end of the Tertiary in other parts of the northern hemisphere.”

Interestingly, the generic similarity between the Clarno Nut Beds flora and that of the Middle Eocene Claiborne Formation of Kentucky and Tennessee is low, including only *Magnolia*, *Nyssa*, †*Paleocarya*, and *Sabal* Adans. (Manchester, 1994). Manchester (1994) suggested that differences in the Clarno and Claiborne floras may have been caused by geographic barriers to dispersal between eastern and western North America, namely the mid-continental Cretaceous sea and high paleoelevations of the southern Rocky Mountains. However, although more limited than in the western United States, there also is fossil evidence for the occurrence of several other boreotropical genera in eastern North America, i.e., *Alangium*, *Ampelopsis* Michx., †*Conarium*, *Engelhardtia* Lesch. ex Blume, *Eucommia* Oliv., *Ficus* L., *Glyptostrobus* Endl., members of Icacinaceae (including *Iodes* Blume), *Nypa* Steck (a mangrove palm), *Platycarya* Siebold & Zucc., *Pterocarya* Kunth, *Pteroceltis* Maxim., *Sargentodoxa* Rehder & E. H. Wilson, *Sciadopitys* Siebold & Zucc., *Sinomenium* Diels, *Symplocos* Jacq., *Tinospora* Miers, *Vitis* L., and †*Wetherellia* (extinct) (Tiffney, 1985b, 1993, 1999; Call & Dilcher, 1997; Manchester et al., 2009; Liu & Jacques, 2010; Stull et al., 2011). Further, molecular phylogenetic data provide evidence that closely related eastern North American–western North American disjunct taxa did not diverge until the Late Miocene or later (Xiang et al., 1998, 2000; see below), indicating that floristic exchange between the two regions continued through the Late Neogene.

The fruit and seed flora of the Early Eocene London Clay of southern England and of the Middle Eocene Messel and Geiseltal floras of continental Europe are other examples of the boreotropical flora. Most of the families and 24% of the Clarno Nut Beds genera occur in these three Early to Middle Eocene floras (Manchester, 1994, and references cited therein). These floristic similarities support other evidence (see Tiffney, 1985a, 1985b, 1994, 1999; Frederiksen, 1988; Manchester et al., 1994; Kvaček et al., 2000; Denk et al., 2010) for the existence of a land connection (most likely across the North Atlantic) between Europe and North America during Early or Middle (and perhaps to the Late, see below) Tertiary. No comparable seed and fruit floras are known from Asia (Manchester, 1994).

EARLY OLIGOCENE MIXED MESOPHYTIC FOREST OF OREGON

ORIGIN

During the Eocene–Oligocene transition (see Prothero, 1994), the global climate changed from warm and equable to cooler, more seasonal (temperate) conditions (Chaney, 1948; Retallack, 1992; Wolfe, 1992; Smith et al., 1998). As a result, the vegetation of central Oregon shifted, through a succession of floristic changes between ca. 39 and 33 Ma, from a paratropical/subtropical rainforest containing many tropical/subtropical elements, e.g., bananas (*Ensete* Horan.), cycads, *Mastixia* Blume, *Meliosma* Blume, palms (*Sabal*), and many lianas in the families Icacinaceae, Menispermaceae, and Vitaceae (Manchester, 1981, 1994, 1995; Wolfe, 1981; Smith et al., 1998) to a temperate broad-leaved deciduous (Mixed Mesophytic) forest (Manchester, 1990, 2000; Meyer & Manchester, 1997). The Early Oligocene Bridge Creek flora (ca. 33 Ma) of Oregon is among the oldest, largest (total minimum taxa of 34 families, 106 genera, and 125 species), and best documented in the middle latitudes of the Northern Hemisphere dominated by broad-leaved deciduous taxa (Manchester & Meyer, 1987; Meyer & Manchester, 1997). This flora differs from that of the Middle Eocene Clarno Nut Beds in its low diversity of both broad-leaved evergreens and lianas. Meyer and Manchester (1997: 51) conclude that this forest “... developed from the congregation of various lineages having origins in older floras of dissimilar character.” They envisioned (1997: 51) “... plant species as having had at least five possible responses to climatic cooling of the Eocene–Oligocene transition: (1) local or global extinction, (2) survival through preadaptation, (3) survival through rapid physiological evolution, (4) dispersal from upland regions, and (5) dispersal of particular species (not whole communities) from higher latitudes.”

RELATIONSHIPS TO PRESENT-DAY FORESTS

Genera of the Bridge Creek flora include those that had become distributed across the Northern Hemisphere by the Early Miocene and are important components in present-day deciduous forests of eastern Asia and eastern North America (e.g., *Acer*, *Aesculus* L., *Betula*, *Carya*, *Cercis* L., *Cornus*, *Fagus*, *Fraxinus* L., *Juglans*, *Liquidambar*, *Ostrya* Scop., *Quercus*, *Tilia*, and *Ulmus*). Many of these genera also occur in Europe. Noteworthy is the occurrence on the escarpment of eastern Mexico (Sierra Madre Oriental) of identical species and species pairs, including *Acer*, *Carpinus*, *Carya*, *Cercis*, *Cornus*, *Fagus*, *Liquidam-*

bar, *Magnolia*, *Nyssa*, *Pinus*, and *Platanus*, that are disjunct from the eastern United States (Miranda & Sharp, 1950; Graham, 1973). Arrival of this Mixed Mesophytic Forest element into eastern Mexico began in the Miocene and had become considerably more diverse by the Pliocene (Graham, 1993b, 1999b, 2010; Ruiz-Sanchez & Ornelas, 2014; Manos & Meireles, 2015). Graham (1999b) noted that the appearance of these temperate species in Mexico, which he envisioned to be due to north to south migration from the eastern United States, was coincident with climate cooling in the Late Cenozoic, beginning in the Middle Miocene (see Graham, 2011; Zachos et al., 2001). Neither Milne and Abbott (2002) nor Milne (2006) included eastern Mexico as an area of disjunct Tertiary relicts, whereas Manos and Meireles (2015) included it as an area of endemism for temperate flora in the Northern Hemisphere.

Phytogeographic patterns of the extant members of this flora include eastern Asian–eastern North American disjuncts (*Catalpa* Scop., *Carya*, *Cladrastis*, *Liquidambar*, and *Menispermum* L.); eastern Asian endemics (*Acuba* Link, *Craigia* W. W. Sm. & W. E. Evans, *Cercidiphyllum*, *Cunninghamia* R. Br. ex A. Rich., *Hovenia* Thunb., *Keteleeria* Carrière, *Metasequoia*, and *Pterocarya*); and eastern North American endemics (*Comptonia* L'Hér. ex Aiton, *Decodon* J. F. Gmel., *Fothergilla* L., and *Pinckneya* Michx.). *Metasequoia* was the dominant conifer in the Bridge Creek flora (Meyer & Manchester, 1997). Further, 86% of the extant genera in this flora are native to eastern Asia today and 68% to eastern North America (Meyer & Manchester, 1997). The Bridge Creek flora was floristically and physiognomically similar to the present-day deciduous forests of eastern Asia and eastern North America. Based on various temperature parameters, the Bridge Creek flora is representative of a Mixed Mesophytic Forest (sensu Wolfe, 1979), but it is near the transition with Mixed Northern Hardwood Forest (cf. Meyer & Manchester, 1997). Although the greatest representation of extant taxa in this flora is in the present-day Mixed Mesophytic Forest of eastern Asia, it has fewer evergreen taxa than the Asian Mixed Mesophytic Forest, and in this respect the Bridge Creek forest was more similar to the present-day Mixed Northern Hardwood Forest (sensu Wolfe, 1979; Meyer & Manchester, 1997) of eastern Asia. According to Meyer and Manchester (1997: 43), “Floristically the Bridge Creek flora is most similar to the Mixed Mesophytic forest [of Southeast Asia] in the presence of *Torreya* [Arn.], *Cunninghamia*, *Keteleeria*, *Cedrela* [P. Browne], *Cercidiphyllum*, and *Pterocarya*. Most of

the other extant genera of the fossil assemblage occur today in both Mixed Mesophytic and Mixed Northern Hardwood forest types.”

MIocene MIXED MESOPHYTIC FORESTS OF OREGON–IDAHO

Floristic elements of the Mixed Mesophytic Forest were present in the western United States until the Middle to Late Miocene (Axelrod, 1992). Characteristic Miocene examples of this microfossil/megafossil flora/vegetation include the Succor Creek flora of eastern Oregon–adjacent Idaho (Taggart & Cross, 1980, 1990; Cross & Taggart, 1982), and the Clarkia (Smiley et al., 1975; Smiley & Rember, 1981; Baghai, 1988; Manchester & Chen, 2006) and Musselshell Creek (Baghai & Jorstad, 1995) floras of northern Idaho. Fossils of the mature forests at these sites represent a gradient of plant communities and successional stages. The Mixed Mesophytic Forest was represented by the mature slope-bottom-land (floodplain) hardwood forest (Fig. 1). Many genera of woody plants (except *Pachysandra* Michx., an herb) in these floras have become extinct in North America and survive only in the Asiatic region, including the Caucasus, the Himalayas, and Malesia (C = Clarkia, MC = Musselshell Creek, SC = Succor Creek). These include *Ailanthus* Desf. (SC), *Cephalotaxus* Siebold & Zucc. ex Endl. (SC), *Cercidiphyllum* (C), *Cunninghamia* (C), *Exbucklandia* R. W. Br. (MC), *Ginkgo* (MC, SC), *Glyptostrobus* (SC), *Keteleeria* (SC), *Metasequoia* (C, MC), *Paliurus* Mill. (C), *Paulownia* Siebold & Zucc. (C), *Platycarya* (MC), *Pterocarya* (C, MC, SC), *Tetracentron* (C), and *Zelkova* (C, MC, SC). Those that became extinct in western North America and survive in both eastern Asia and eastern North America include *Carya* (C, MC, SC), *Gordonia* (C), *Halesia* (C), *Hamamelis* (C), *Lindera* Thunb. (C, MC), *Liriodendron* (C), *Magnolia* (C, MC, SC), *Nyssa* (C, SC), *Pachysandra* (SC), and *Sassafras* J. Presl (C, SC) (Taggart & Cross, 1980; Smiley & Rember, 1981; Golenberg et al., 1990; Baghai & Jorstad, 1995); all of these latter genera except *Gordonia* occur in Kentucky. However, *Gordonia*, as *G. lasianthus* (L.) J. Ellis, does remain to the southeast of Kentucky, on the Atlantic and Gulf coastal plains of North Carolina to southern Florida and west to southeastern Louisiana (Seiler et al., 2015). *Comptonia* is the only present-day endemic genus in eastern North America that was present in these Miocene forests. Other genera in the Clarkia, Musselshell Creek, and/or Succor Creek floras present in the forests of Kentucky today but that no longer occur in western North America include the vines *Ampelopsis*, *Berchemia* Neck. ex DC., and *Cocculus*; the shrubs *Asimina* Adans. and

MONTANE CONIFER

PINE-MIXED HARDWOOD

SLOPE-BOTTOMLAND
HARDWOOD
(Mixed Mesophytic Forest)RIPARIAN
THICKET

MARSH

LAKE

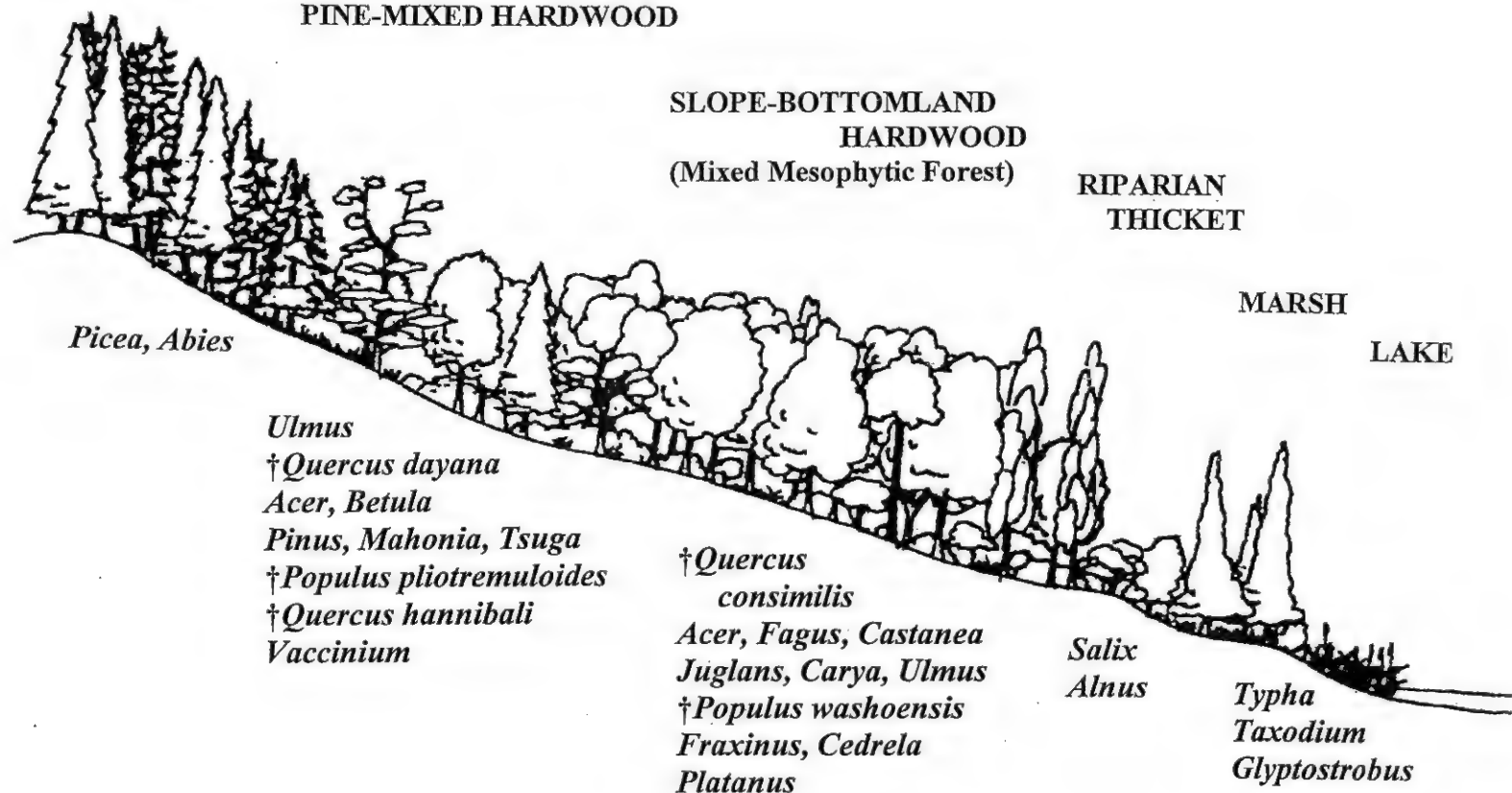


Figure 1. Generalized reconstruction of the Middle Miocene mature closed-canopy (climax) vegetation at Succor Creek, eastern Idaho–adjacent Oregon. Mixed Mesophytic forest is represented by the slope-bottomland hardwood portion of the gradient. Adapted from Cross and Taggart, 1982: 693, with permission for re-use from the Missouri Botanical Garden Press, St. Louis.

Hydrangea; and the trees *Carpinus*, *Castanea* Mill., *Diospyros*, *Fagus*, *Gleditsia* J. Clayton, *Gymnocladus* Lam., *Ilex* L., *Liquidambar*, *Ostrya*, *Taxodium* Rich., *Tilia*, and *Ulmus*.

LATE CRETACEOUS AND TERTIARY VEGETATION OF THE
EASTERN UNITED STATES

Compared to the Pacific Northwest, macrofossil data from which to reconstruct the Tertiary history of the Mixed Mesophytic Forest in eastern North America are meager (Graham, 1964, 1993a, 1999a; Wallace & Wang, 2004). Only a few relatively diverse fossil macrofloral assemblages are known in which a high percentage of the taxa have been identified accurately (see Dilcher, 1971). Macrofloral assemblages relevant to reconstruction of the Tertiary vegetation of the eastern United States include the Middle Eocene Claiborne flora of the upper portion of the Mississippi Embayment of Kentucky and Tennessee (Table 2); the Late Oligocene or Early Miocene Brandon lignite flora of Vermont (Tiffney, 1994; the middle Early Miocene, sensu Traverse, 1994); the Late Miocene Brandywine flora of the southern Maryland Coastal Plain (McCartan et al., 1990); the Early Eocene fruit and seed flora from the Fisher/Sullivan site in coastal eastern Virginia (Tiffney, 1999); and the Late Miocene/Early Pliocene Gray Fossil Site in northeastern Tennessee (Gong et al., 2010; Liu & Jacques, 2010).

Frederiksen (1989) used a combination of microfossils (pollen) and macrofossils (fruits, seeds, leaves, and wood) to reconstruct what he thought was probably the Late Cretaceous–Tertiary vegetation of New England, but there are many gaps in the fossil record on which this reconstruction is based. The Mixed Mesophytic Forest has been shown to be present in New England from the Middle Oligocene to the Late Miocene (Frederiksen, 1989). This fossil flora included genera that occur in present-day temperate deciduous forests of eastern North America (e.g., *Betula*, *Carya*, *Castanea*, *Fagus*, *Gordonia*, *Juglans*, *Liquidambar*, *Nyssa*, *Platanus*, *Quercus*, and *Tilia*) as well as Asian exotics that have been extirpated from North America and survive only in eastern Asia (i.e., *Alangium*, *Glyptostrobus*, *Pterocarya*, *Sargentodoxa*, and *Sciadopitys*). Frederiksen's study contains the only diagram we are aware of that heretofore illustrates the sequence of Late Cretaceous–Tertiary vegetation in eastern North America.

LATE CRETACEOUS AND TERTIARY VEGETATION OF KENTUCKY

Although Late Cretaceous (Maestrichtian) strata occur in western Kentucky (Olive, 1980; McDowell, 1986), and many representatives of the †Normapolles palynoflora have been collected from them, no megafloral assemblage has been found in these sediments. However, two studies in the adjacent states of Illinois and Tennessee provide information

Table 2. Some Tertiary megafossils from western Kentucky–Tennessee. Most of the taxa were collected only from the Middle Eocene Claiborne Formation. Fossil species names (and occasional genus names if no extant species) indicated by a dagger.

Family	Taxon	References
GYMNOSPERMS		
Podocarpaceae	<i>Podocarpus</i> Labill. sect. <i>Stachycarpus</i> Endl.	Dilcher, 1969
	<i>Podocarpus</i> sect. <i>Podocarpus</i> , sp. indet.	Moore et al., 2003
ANGIOSPERMS, MONOCOTS		
Araceae	† <i>Acorites heeri</i> <i>Philodendron limnestis</i>	Crepet, 1978 Dilcher & Daghljan, 1977
Palmae	† <i>Amesoneuron</i> , sp. indet.	Daghljan, 1978
	† <i>Costapalma philipii</i>	Daghljan, 1978
	† <i>Eopalma fibrosa</i>	Grote, 1989
	† <i>Palmacites eocenica</i>	Daghljan, 1978
	† <i>Palustrapalma agathae</i>	Daghljan, 1978
	† <i>Sabal dortchii</i>	Daghljan, 1978
	† <i>Sabalites grayanus</i>	Daghljan, 1978
	Palm	Moore et al., 2003
Poaceae	Grass	Crepet & Feldman, 1991
Smilacaceae	<i>Smilax</i> L., two sp. indet.	Dilcher & Lott, 2005
	<i>Smilax</i>	Moore et al., 2003
ANGIOSPERMS, DICOTS		
Altingiaceae	<i>Liquidambar</i> L., sp. indet.	Dilcher & Lott, 2005
Anacardiaceae (tribe Spondideae) or Humeriaceae (?)	† <i>Campanurbia lenticularis</i>	Grote, 1989
Annonaceae	† <i>Duguetia leei</i>	Roth, 1981
	<i>Duguetia</i> A. St.-Hil., sp. indet.	Dilcher & Lott, 2005
	<i>Duguetia</i> , two sp. indet.	Moore et al., 2003
Apocynaceae	† <i>Apocynophyllum</i> , sp. indet.	Dilcher & Lott, 2005
	† <i>Apocynophyllum mississippiens</i>	Moore et al., 2003
Araliaceae	† <i>Dendropanax eocenensis</i>	Dilcher & Dolph, 1970; Dilcher & Lott, 2005
	<i>Dendropanax</i> Decne. & Planch., two sp. indet.	Moore et al., 2003
Cannabaceae (including Celtidaceae)	† <i>Pteroceltis knowtonii</i>	Manchester et al., 2009
Ceratophyllaceae	<i>Ceratophyllum muricatum</i> Cham. subsp. †incertum	Herendeen et al., 1990
Eucommiaceae	† <i>Eucommia eocenica</i>	Call & Dilcher, 1997
	<i>Eucommia</i> Oliv., sp. indet.	Moore et al., 2003
Euphorbiaceae, Euphorbioideae	† <i>Crepetocarpon perkinsii</i>	Dilcher & Manchester, 1988
	† <i>Hippomaneoida warmanensis</i>	Crepet & Daghljan, 1982
Fagaceae, Castaneoideae	† <i>Castaneoidea puryearensis</i>	Crepet & Daghljan, 1980
	† <i>Castaneophyllum tennesseensis</i>	Jones & Dilcher, 1988
	† <i>Castaneophyllum moorii</i>	Jones & Dilcher, 1988
	† <i>Castanopsoidea columbiana</i>	Crepet & Nixon, 1989
	† <i>Paleojulacea laxa</i>	Crepet & Nixon, 1989
Fagaceae, Fagoideae	† <i>Trigonobalanoidea americana</i>	Crepet & Nixon, 1989
	† <i>Berryophyllum warmanense</i>	Jones & Dilcher, 1988
Fagaceae, Quercoideae	† <i>Berryophyllum saffordii</i>	Jones & Dilcher, 1988
	† <i>Berryophyllum tenuifolium</i>	Jones & Dilcher, 1988; Dilcher & Lott, 2005
	† <i>Berryophyllum</i> , sp. indet.	Dilcher & Lott, 2005
	† <i>Knightiophyllum wilcoxianum</i>	Dilcher & Mehrotra, 1969; Moore et al., 2003; Dilcher & Lott, 2005
	† <i>Corylopsis americana</i>	Grote, 1989

Table 2. Continued.		
Family	Taxon	References
Icacinaceae	† <i>Natsiatum wilcoxiana</i>	Stull et al., 2011
	† <i>Phytocrene densipunctata</i>	Stull et al., 2011
Juglandaceae	† <i>Eokachyra aeolius</i>	Crepet et al., 1975
	† <i>Eoengelhardia puryearensis</i>	Crepet et al., 1980
	† <i>Oreoroa claibornensis</i>	Dilcher & Manchester, 1986
	† <i>Oreoroa</i> , sp. indet.	Moore et al., 2003
	† <i>Paleocarya puryearensis</i>	Manchester, 1987
	† <i>Paleooreomuunnea stoneana</i>	Dilcher et al., 1976
	† <i>Paraengelhardia eocenica</i>	Berry, 1916; Manchester, 1987
	† <i>Paraengelhardia</i> , sp. indet.	Moore et al., 2003
	† <i>Androglandula tennesseensis</i>	Taylor, 1988b
	<i>Ocotea obtusifolia</i> Kunth	Dilcher, 1963a
Lauraceae	<i>Ocotea</i> Aubl., sp. indet.	Dilcher & Lott, 2005
	<i>Persea</i> Mill., two spp. indet.	Moore et al., 2003
	cf. <i>Acrocarpus</i> Wight ex Arn., sp. indet.	Herendeen, 1992
	<i>Caesalpinia</i> L. subg. <i>Caesalpinia</i>	Herendeen, 1992
Leguminosae, Caesalpinioideae	<i>Caesalpinia</i> subg. <i>Mezoneuron</i> (Desf.) Vidal ex Herend. & Zarucchi	Herendeen & Dilcher, 1991
	† <i>Caesalpinia claibornensis</i> Herend. & Dilcher	
	cf. Caesalpinioideae	Herendeen, 1992
	<i>Caesalpinia</i> , sp. indet.	Moore et al., 2003
	† <i>Leguminosites prefoliatus</i>	Herendeen, 1992
	cf. † <i>Leguminosites ingafructoides</i>	Herendeen, 1992
	cf. † <i>Leguminosites phyllocarpoides</i>	Herendeen, 1992
	cf. <i>Erythrophleum</i> Afzel. ex R. Br., sp. indet.	Herendeen, 1992
	† <i>Crudia grahamiana</i>	Herendeen & Dilcher, 1990a
	<i>Senna</i> Mill., sp. indet.	Herendeen, 1992
	cf. <i>Stemonocoleus</i> Harms/ <i>Aubrevillea</i> Pellegr.	Herendeen, 1992
Leguminosae, Mimosoideae	† <i>Eomimosoidea plumose</i>	Crepet & Dilcher, 1977
	† <i>Duckeophyllum eocenicum</i>	Herendeen & Dilcher, 1990b
	† <i>Eliasofructus catahoulensis</i>	Herendeen & Dilcher, 1990b
	† <i>Eliasofructus claibornensis</i>	Herendeen & Dilcher, 1990b
	† <i>Parvileguminophyllum georgianum</i>	Herendeen & Dilcher, 1990b
	† <i>Protomimosoidea buchananensis</i>	Crepet & Taylor, 1986
Leguminosae, Papilionoideae	† <i>Barnebyanthus buchananensis</i>	Crepet & Herendeen, 1992
	cf. <i>Cladrastis</i> Raf., sp. indet.	Herendeen, 1992
	cf. <i>Cladrastis</i>	Dilcher & Lott, 2005
	† <i>Diplostropis claibornensis</i>	Herendeen & Dilcher, 1990c
	cf. † <i>Gleditsia?</i> <i>mississippiensis</i>	Herendeen, 1992
	† <i>Gleditsiophyllum eocenicum</i>	Herendeen, 1992
	cf. <i>Machaerium</i> Pers., sp. indet.	Herendeen, 1992
	cf. <i>Ormosia</i> Jacks., two or three sp. indet.	Herendeen, 1992
	cf. <i>Ormosia</i> , sp. indet.	Dilcher & Lott, 2005
	<i>Ormosia</i> , sp. indet.	Moore et al., 2003
	cf. <i>Sophora</i> L. subg. <i>Styphenolobium</i>	Herendeen, 1992
	cf. Sophoreae	Herendeen, 1992
	cf. <i>Swartzia</i> Schreb., two or three sp. indet.	Herendeen, 1992
	<i>Swartzia</i> , sp. indet.	Dilcher & Lott, 2005
	<i>Swartzia</i> , sp. indet.	Moore et al., 2003
Magnoliaceae	† <i>Magnolia tiffneyi</i>	Grote, 1989
	† <i>Magnolia kentuckyensis</i>	Grote, 1989

Table 2. Continued.

Family	Taxon	References
Malpighiaceae	† <i>Eoglandulosa warmanensis</i>	Taylor & Crepet, 1987
Moraceae	† <i>Cornerocarpon copiosum</i>	Grote, 1989
	† <i>Cornerocarpon crassibracteatum</i>	Grote, 1989
	cf. <i>Ficus</i> L., sp. indet.	Dilcher & Lott, 2005
	† <i>Pseudomedia</i> , sp. indet.	Dilcher & Lott, 2005
Myricaceae	<i>Myrica</i> L., sp. indet.	Dilcher & Lott, 2005
Myrtaceae	† <i>Syzygiodes</i> , sp. indet.	Moore et al., 2003
Nyssaceae	† <i>Nyssa eolignitica</i>	Dilcher & McQuade, 1967
	<i>Nyssa</i> L., sp. indet.	Moore et al., 2003
Oleaceae	† <i>Fraxinus wilcoxiana</i>	Call & Dilcher, 1992
	Oleaceae leaf morphotype	Dilcher & Lott, 2005
Platanaceae	<i>Platanus</i> L., sp. indet.	Dilcher & Lott, 2005
Rhamnaceae	† <i>Berhamniphyllum claibornense</i>	Jones & Dilcher, 1980; Dilcher & Lott, 2005
	† <i>Berhamniphyllum</i> , sp. indet.	Dilcher & Lott, 2005
Rosaceae	—	Moore et al., 2003
Rubiaceae	† <i>Paleorubiaceophyllum eocenicum</i> var. <i>eocenicum</i>	Roth & Dilcher, 1979
	† <i>Paleorubiaceophyllum eocenicum</i> var. <i>amplum</i>	Roth & Dilcher, 1979
	† <i>Paleorubiaceophyllum eocenicum</i> var. <i>lawrensis</i>	Roth & Dilcher, 1979
	cf. † <i>Paleorubiaceophyllum</i> , sp. indet.	Dilcher & Lott, 2005
Salicaceae	<i>Populus</i> L., sp. indet.	Dilcher & Lott, 2005
Sapindaceae	† <i>Cupanites</i> , sp. indet.	Dilcher & Lott, 2005
	<i>Sapindus</i> L., sp. indet.	Moore et al., 2003
Sapotaceae	† <i>Platyulota kentuckyensis</i>	Grote, 1989
	† <i>Sapotispermum cucullatum</i>	Grote, 1989
Theaceae	† <i>Ternstroemites</i> , sp. indet.	Dilcher & Lott, 2005
Theaceae, Camelloideae, Gordonieae	† <i>Andrewsiocarpus henryense</i>	Grote, 1989
	† <i>Gordonia lamkinensis</i>	Grote & Dilcher, 1992
	† <i>Gordonia warmanensis</i>	Grote & Dilcher, 1992
	<i>Gordonia</i> J. Ellis, sp. indet.	Grote, 1989
	cf. <i>Gordonia</i> , sp. indet.	Dilcher & Lott, 2005
	<i>Gordonia</i> , sp. indet.	Moore et al., 2003
	† <i>Gordoniopsis polysperma</i>	Grote & Dilcher, 1992
Ulmaceae, Celtidoideae	† <i>Eoceltis dilcheri</i>	Zavada & Crepet, 1981

relevant to a description of the Late Cretaceous vegetation of Kentucky. Wheeler et al. (1987) described five species of fossil dicotyledonous woods from the McNairy Formation (Maestrichtian) in southern Illinois, which also occurs in Kentucky: †*Paraquercinum cretaceum* (similar to the evergreen oak *Lithocarpus* Blume, Fagaceae), †*Paraphyllanthoxylon illinoense* (most likely a phyllanthoid Euphorbiaceae s.l.), †*Icacinoxylon alternipunctata* (affinity appears to be with Icacinaceae); †*Parabombacaceoxylon magniporosum* (likely Bombacaceae); and †*Parapocynaceoxylon barghoorni* (likely Apocynaceae). None of these five species had growth rings, which infers a non-seasonal climate. Further, all five would have had a high vulnerability (to air embolisms, caused by drought or freezing tempera-

tures) index (V), where $V = d/D$, d is mean vessel diameter, and D = mean number of vessels/mm² (Carlquist, 1977), indicating these taxa did not experience water stress and had low-density wood, a characteristic of fast-growing woody plants. Thus, it seems likely that these were colonizing species in a lowland to middle-elevation tropical rainforest (Wheeler et al., 1987).

In another study of fossil plant material from the McNairy Formation, Wolfe and Upchurch (1987) analyzed leaf physiognomy and wood structure of specimens collected by E. W. Berry (1916) in Tennessee, as part of their effort to describe climate and vegetation of the Late Cretaceous in North America. They concluded that the climate was subhumid megathermal (mean annual temperature

> 20°C) with a mean annual rainfall < 1650 mm and little seasonality in either temperature or precipitation. The vegetation was described as open-canopy, broad-leaved, evergreen woodland without lianas and not multistratal. The leaves were small (i.e., low size index), generally lacked drip-tips, and 62%–69% of them had entire margins. The wood had a high vulnerability index and a high water-conducting capability, and lacked growth rings.

Horrell (1991) used preserved climatic indicators, including paleofloras, evaporite deposits, and coal deposits, to reconstruct world climates and terrestrial biomes in the latest Cretaceous (Maestrichtian). He recognized seven biomes. Kentucky is located in Biome 4, (winter-wet), a winter-wet, summer-dry climate with sclerophyllous-leaved vegetation consisting of shrubs and small trees and with conifers common. In their study of world terrestrial vegetation and its effects on climate during the Maestrichtian, Otto-Bliesner and Upchurch (1997) and Upchurch et al. (1998, 1999) also recognized seven biomes. Kentucky is located in their Biome 3, subtropical broad-leaved evergreen forest and woodland, an angiosperm-dominated vegetation with palms and gingers, in addition to cold-sensitive fungal taxa.

The only Tertiary macrofossil floral assemblage in Kentucky is that of the Middle Eocene Claiborne Group of the Mississippi Embayment of the Gulf Coastal Plain in western Kentucky and adjacent portions of western Tennessee. Thus, the Tertiary vegetation of Kentucky is somewhat speculative. Although the Middle Eocene boreotropical flora of the Clarno Nut Beds of Oregon contains many genera from the Mixed Mesophytic Forest (Manchester, 1994), the Claiborne flora of Tennessee and Kentucky represents a semideciduous tropical dry forest with a high number of Leguminosae (Herendeen, 1992; Graham & Dilcher, 1995; Graham, 1999a; cf. Table 2). According to Graham (1999a), the Paleocene to Early Eocene tropical rainforest in the southeastern United States was replaced by tropical dry forest in response to a decrease in amount and an increase in seasonality of rainfall.

Based on the distribution of closely related extant taxa, Herendeen (1992) recognized four biogeographic patterns among Leguminosae in the Claiborne flora: (1) tropical South America, e.g., *Diploptropis* Benth., (2) tropical Asia and Africa, e.g., *Caesalpinia* L. subg. *Mezoneuron* (Desf.) Vidal ex Herend. & Zarucchi, (3) pantropical, e.g., *Crudia* Schreb. (Herendeen & Dilcher, 1990a), and (4) temperate North America–temperate Asia, e.g., *Cladrastis*. *Cladrastis* (Herendeen, 1992) and *Diploptropis* (Herendeen & Dilcher, 1990b) are extant genera, and

Caesalpinia subg. *Mezoneuron* (Herendeen & Dilcher, 1991) is an extant subgenus, all of which date back to the Middle Eocene. Herendeen (1992: 150) stated that “When [the Leguminosae are] taken together with the fossil record of other families from the Mississippi Embayment, it is evident that many of the fossils are related to taxa restricted to South America today.” He suggested that the high representation of South American taxa in this fossil flora is due to their dispersal from tropical South America during the Late Cretaceous and Paleogene (Herendeen, 1992; Herendeen et al., 1992).

Taylor (1988a; also see Taylor, 1990) analyzed reports of Early Tertiary plant fossils from the southeastern United States in relation to the phylogeny and present-day geographic distribution of extant relatives and fossil records outside North America. He concluded that (1) the Paleogene tropical flora of the southeastern United States contained both boreotropical and West Gondwanaland elements, and (2) there was bidirectional, perhaps more so to the north, interchange of taxa between North and South America in the Late Cretaceous–Early Tertiary via the proto-Caribbean sea. South America was isolated from other land masses from the Late Cretaceous to the Middle Pliocene. Undoubtedly, there were Gondwanan elements in the southeastern United States in the Early Tertiary. For example, macrofossils of *Podocarpus* sect. *Stachycarpus* Endl. (a gymnosperm) and of *Duguetia* A. St.-Hil. (Annonaceae) have been collected from the Claiborne Formation (Dilcher, 2000).

Following the Eocene, rainfall in the southeastern United States increased as a result of continued uplift of the Rocky Mountains, which in turn caused changes in atmospheric circulation that brought warm, moist winds from the Gulf of Mexico. Consequently, the gradual disappearance of the tropical dry forest favored the development of the Eastern Deciduous Forest. Graham (1999a: 232) characterized the vegetation of the southeastern United States during the Oligocene as “Tropical” on the coast, “Tropical toward deciduous (mixed mesophytic)” inland, and “Deciduous (mixed mesophytic)” in uplands; and that of the Early Miocene was “Warm-temperate to subtropical?” Graham also noted that by the Middle and Late Eocene floristic elements already were available for vegetation associations found today in the southeastern United States.

Graham (1999a: 266) summarized the development of the vegetation of this region from Middle Miocene (apparently) through the Pliocene as follows.

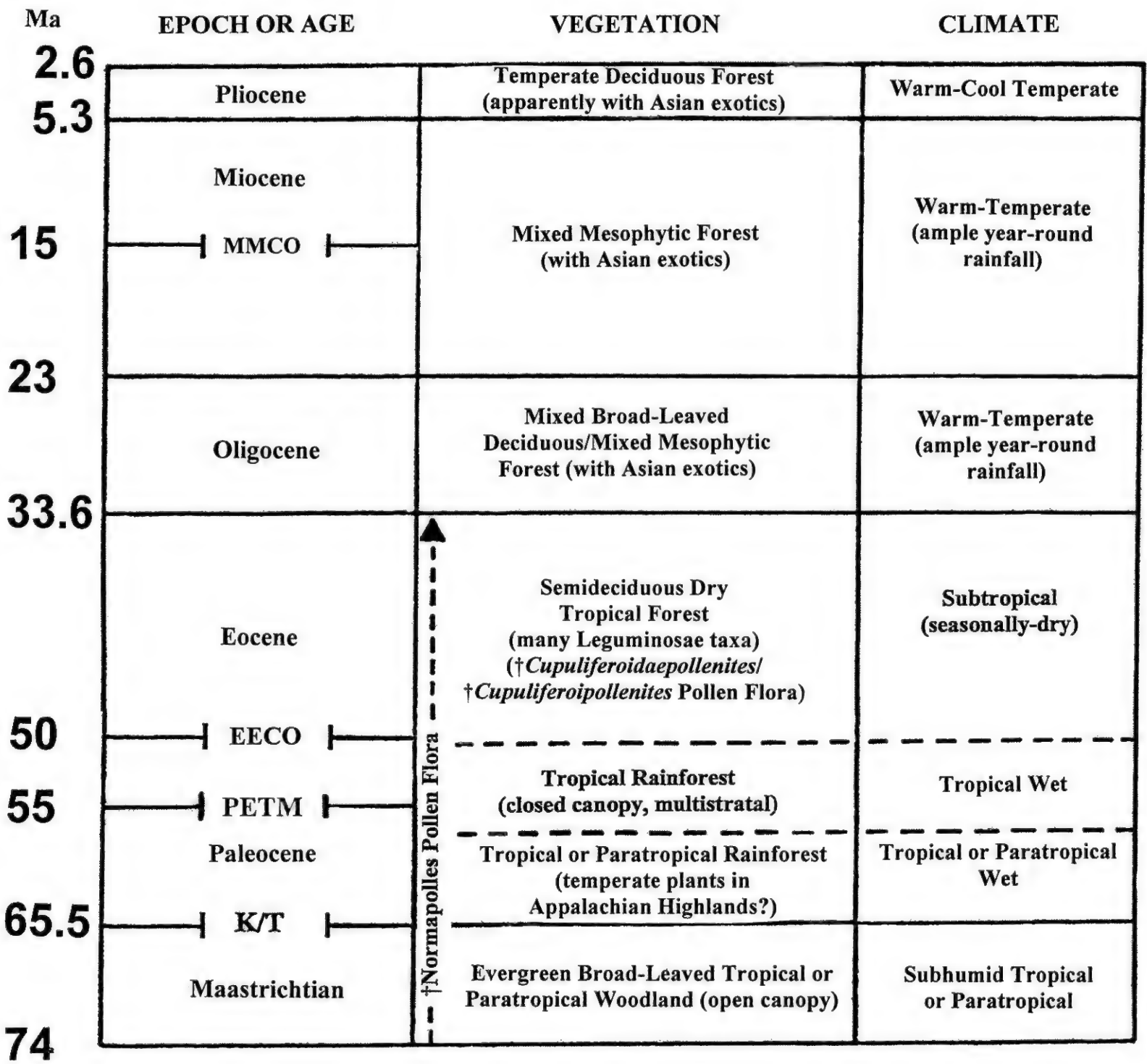


Figure 2. Inferred Late Cretaceous and Tertiary climax vegetation and climate of Kentucky constructed from numerous sources, including Graham (1999a). K/T refers to the Cretaceous–Tertiary boundary, PETM to the Paleocene–Eocene Thermal Maximum, EECO to the Early Eocene Climatic Optimum, and MMCO to the Middle Miocene Climatic Optimum.

“Although published information of vegetational history is surprisingly meager for the Middle Miocene through the Pliocene of the southeastern United States [see Wallace & Wang, 2004; Ochoa et al., 2012], it is likely that modernization of the vegetation [of the southeastern United States] accelerated with the Middle to Late Miocene cooling event.[...] The principal effects were the disappearance of most Asian and neotropical exotics by the Pliocene [see Liu & Jacques (2010) and Ochoa et al. (2012), who report *Pterocarya*, *Sargentodoxa*, and *Sinomenium* from the Miocene-earliest Pliocene (7–4.5 Ma) Gray Fossil Site in northeastern Tennessee, for which the palynoflora is dominated by *Carya*, *Quercus*, and *Pinus*], modernization and expansion of the mixed mesophytic forest, the temporal association of different forest genera to constitute various other deciduous forest associations, and development of the Appalachian coniferous forest. In Chapter 6, it was noted that by Claiborne (Middle Eocene)–Jackson (Late Eocene) time, elements [taxa; e.g., see Gray, 1960; Graham, 1972] were available for

assemblage into the mixed mesophytic, southern mixed hardwood, oak–hickory, oak–chestnut, sandpine scrub (*Pinus*, *Sabal*, other rosette palms), flood-plain (*Taxodium*, *Nyssa*), and mangrove (*Acrostichum* [a fern], *Nipa* [*Nypa*, a palm]) associations.”

Thus, by the Early Tertiary many elements of today’s Mixed Mesophytic Forest were present (but not dominant) in the warm temperate to tropical broad-leaved evergreen forests of the southeastern United States (Gray, 1960; Graham, 1972). As such, the origin of the mixed mesophytic forests can be traced to the Early Eocene (Graham, 1972).

Using information in the literature, we have made an attempt to reconstruct the Late Cretaceous and Tertiary vegetation of Kentucky (Fig. 2). Except for the †Normapolles (Tschudy, 1970, 1981) and †*Cupuliferoideaepollenites*/†*Cupuliferoipollenites* pollen

floras (Potter, 1976, 1977; Hower et al., 1990), the main sources of this information were Graham (1999a) and the many references cited in this book. Thus, the open-canopy tropical or paratropical woodland of the latest Cretaceous changed to a tropical or paratropical rainforest (perhaps with temperate plants in the Appalachian Uplands) in the earliest Tertiary (Paleocene); to a closed canopy wet tropical rainforest with multiple strata in the Late Paleocene; to a semi-deciduous dry tropical forest with many Leguminosae in the Middle Eocene (Claiborne Flora); to a broad-leaved deciduous forest with several Asian exotics following the Eocene–Oligocene climatic cooling period; to a Mixed Mesophytic Forest by the Miocene; to a cooler-climate temperate deciduous forest in the Pliocene following further climatic cooling, with which Asian exotics persisted until at least the Late Miocene–Early Pliocene (Liu & Jacques, 2010; Ochoa et al., 2012).

Angiosperm pollen of the †Normapolles complex/type has been found in Late Cretaceous and Paleogene sediments of the Mississippi Embayment portion of Kentucky and adjacent parts of Tennessee (Tschudy, 1970, 1981, 1984). This pollen type, which appears to belong to a core Fagales clade comprising the extant families Betulaceae, Casuarinaceae, Ticodendraceae, Myricaceae, Rhoipetelaceae, and Juglandaceae (Wolfe, 1974; Friis, 1983; Batten, 1989; Sims et al., 1999; Schönenberger et al., 2001; Friis et al., 2003, 2006; Hermanova et al., 2011), first appeared in the Cenomanian, reached peak abundance in the Late Campanian–Maestrichtian, and then declined to extinction by the latest Eocene or Early Oligocene. Thus, during the latest Cretaceous, Kentucky was in the Normapolles Palynofloral Province (Fig. 3), which included eastern North America and western-central Europe (e.g., Srivastava, 1978; Herngreen & Chlonova, 1981; Batten, 1984; Krutzsch & Pacltova, 1987–1988; Herngreen et al., 1996). Two other names used for this region are the North Atlantic–European Province (Muller, 1970) and Euramerian–Turonian Region (Samoylovich, 1977).

In addition to the †Normapolles pollen type, pollen of other angiosperms and of gymnosperms and spores of pteridophytes, bryophytes, and fungi have been found in the latest Cretaceous–Paleogene of the northern portion of the Mississippi Embayment (Jackson Purchase physiographic region) in Kentucky and Tennessee (Dilcher, 1963b, 1965; Elsik & Dilcher, 1974; Potter, 1976; Hower et al., 1990). Elsik and Dilcher (1974) identified palynomorphs of various fungi, ferns, gymnosperms, and dicotyledonous and monocotyledonous angiosperms from upper-

most Claiborne sediments (sensu Potter, 1976) in Lawrence clay pit in Henry County, Tennessee, which adjoins Calloway County, Kentucky. An interesting aspect of their study was the presence of the boreotropical genera (Asian exotics) *Sciadopitys*, *Engelhardia*, and *Platycarya*. Pollen assemblages of both the clay and lignite zones of the Claiborne Formation in the Miller clay pit in Henry County, Tennessee, were dominated by species of †*Cupuliferoideaepollenites* and †*Cupuliferoipollenites* (Potter, 1976), non-magnoliid eudicots, perhaps with affinity to the Fagaceae (Hower et al., 1990). These two pollen genera also were found to be quite abundant in lignite deposits of the Claiborne Formation at several sites in the Jackson Purchase of Kentucky (Hower et al., 1990). However, a considerable number of other pollen morphs were present in the Claiborne Formation, and thus the diversity of this angiosperm-dominated floral assemblage that grew in a warm-temperate to subtropical environment are represented (Potter, 1976; Hower et al., 1990). Based on foliar physiognomy and the temperature limits of palms, Greenwood and Wing (1995) inferred a mean annual, a mean annual range, and a cold-month mean Middle Eocene temperature of 23.9°C, 10.2°C, and 16.1°C, respectively, at a Claiborne site in Henry County, Tennessee. †*Cupuliferoideaepollenites* and †*Cupuliferoipollenites* also were present in notable abundance in lignites of the uppermost Cretaceous–Paleocene McNairy Formation in Kentucky.

MIDDLE AND EARLY CRETACEOUS PALYNOFLORAL PROVINCES THAT INCLUDED KENTUCKY

In the Middle Cretaceous, Kentucky was located in the Southern Laurasian Palynofloral Province (Brenner, 1976; Srivastava, 1981; Batten, 1984; see also Crane, 1987) or Palynofloral Realm (Batten & Wenben, 1987) (Fig. 4). In both North America and Europe, this province was characterized by a high diversity of Pteridophyta, especially ferns in the Schizaeaceae and Gleicheniaceae, and of bisaccate pollen-producing gymnosperms in the Pinaceae and Podocarpaceae. Further, “*Classopollis* [pollen of Cheirolepidaceae, an extinct family of conifers] occurs regularly and may be numerous, and *Araucariacites* is consistently recorded” (Batten, 1984: 136). Land-plant dominance by this pteridophyte/gymnosperm complex of the Middle Cretaceous (Albian–Cenomanian) gave way to the angiosperms by the Late Cretaceous (Brenner, 1976). In terms of both taxonomic diversity and abundance, angiosperms dominate the megafossil flora by the Cenomanian (earliest Late Cretaceous) and also the microfossil

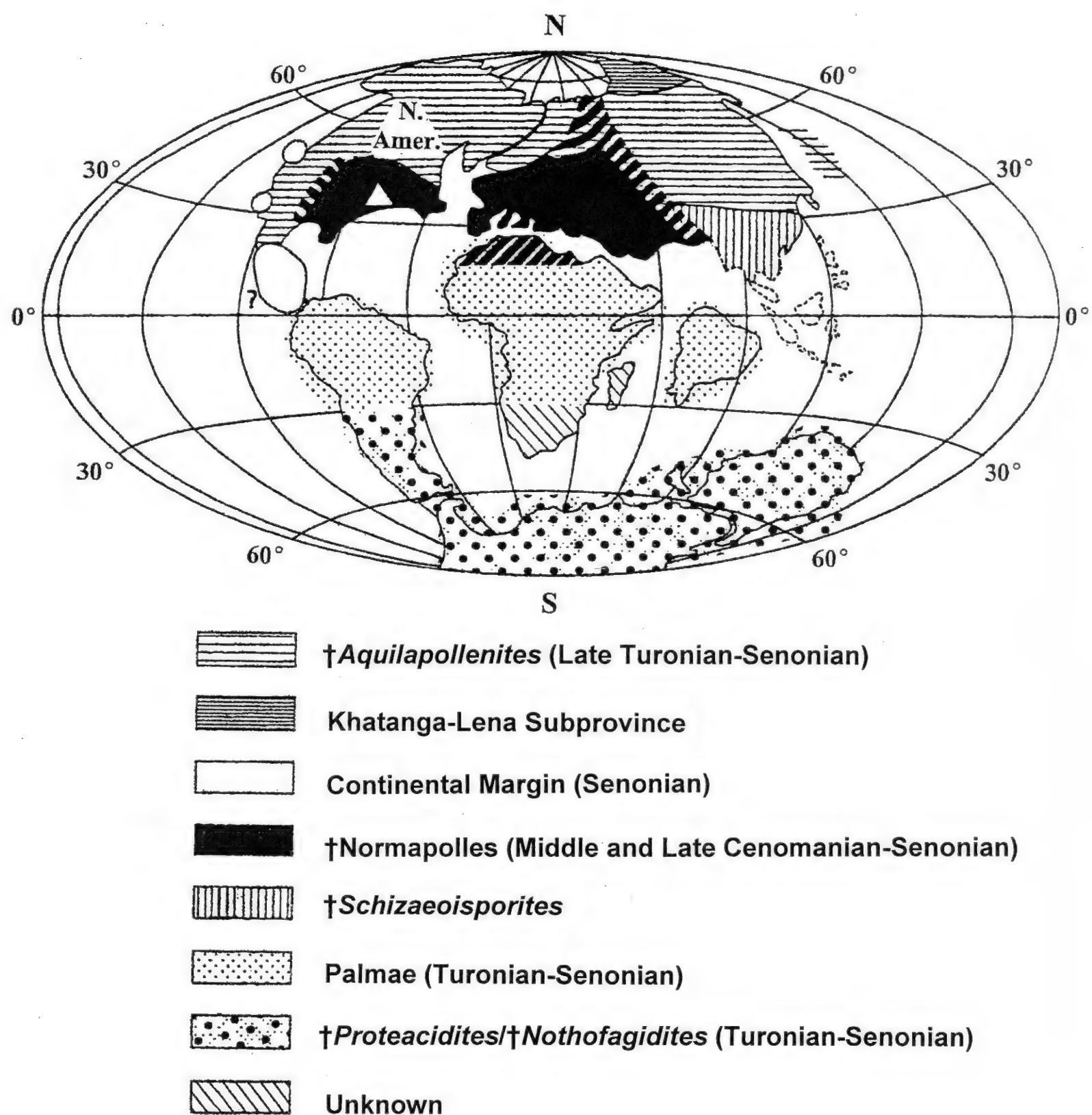


Figure 3. Late Cretaceous palynofloral provinces of the world. Open triangle shows approximate location of Kentucky in the †*Normapolles* Palynofloral Province (from Herngreen et al., 1996: 1162, with permission for re-use from the American Association of Stratigraphic Palynologists Foundation, Dallas, Texas, <www.schweizerbart.de>).

(palynomorph) flora by the Maestrichtian (latest Cretaceous). The increase in diversity and abundance of angiosperms through the Cretaceous was accompanied by decreases in these measures for gymnosperms and free-sporing plants, especially a decrease in abundance of the former and a decrease in diversity of the latter (Crane, 1987; Lidgard & Crane, 1988, 1990; Lupia et al., 1999, 2000; Peralta-Medina & Falcon-Lang, 2012). Boulter et al. (1998) identified major radiations of the angiosperms at around the Cenomanian/Turonian boundary (90 Ma) and at the Cretaceous/Tertiary boundary (65.5 Ma).

On a world map of the Middle Cretaceous (Barremian–Aptian), Srivastava (1994) recognized three palynoflora provinces: Boreal (most of Northern Hemisphere); Equatorial (elater-bearing pollen of unknown affinity, but possibly with Ephedraceae) (Herngreen et al., 1996); and Austral (post-Gondwanaland southern South America, Antarctica, and Australia). Kentucky was located on or near the boundary of the Boreal and Equatorial Provinces. The Elater-Bearing Palynoflora Province replaced the †*Dicheiropollis* Province of the Early Cretaceous. The Elater-Bearing Pollen Province includes the southern part of Brenner's (1976) South Laurasian

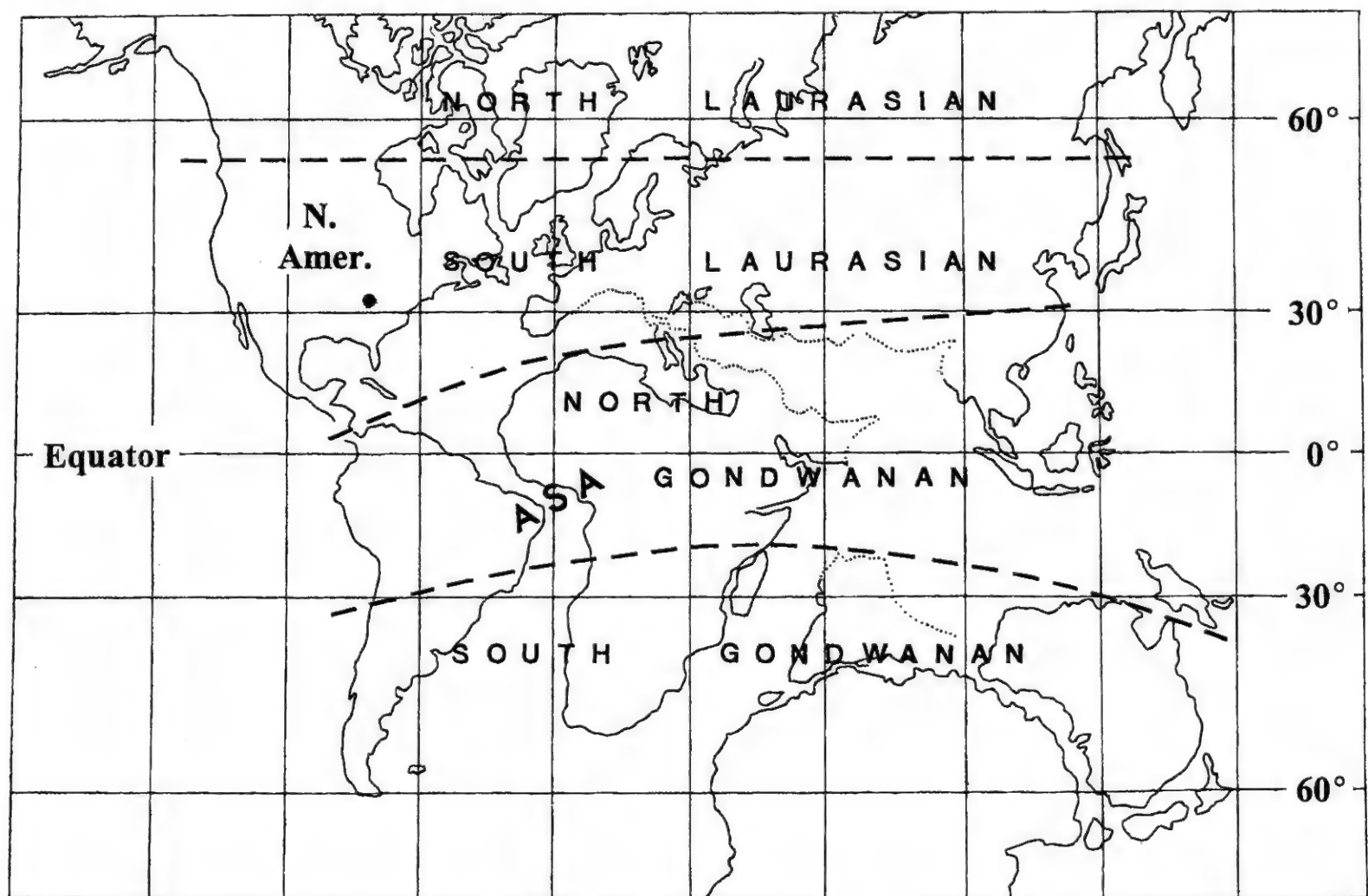


Figure 4. Middle Cretaceous Palynofloral Realms of the world. Longitudinal lines are at 30° intervals. ASA refers to the African/South American Province within the North Gondwanan Realm. Solid circle in North America shows approximate location of Kentucky. From Batten and Wenben, 1987: 223, with permission for re-use from Schweizerbart Scientific Publishers Permissions, Stuttgart, Germany).

Palynofloral Province and most of his North Gondwana Province (Fig. 4).

Finally, in the Early Cretaceous, when angiosperms first appeared in the fossil record (Hickey & Doyle, 1977; Wing & Boucher, 1998; Lupia et al., 1999), Kentucky was located in the southern portion of the Boreal or †*Cerebropollenites* Province (Herngreen & Chlonova, 1981; Herngreen et al., 1996). This province included most of the Northern Hemisphere: North America, Europe, and Asia; it did not include Italy, India, or the Indonesian-Philippine Archipelago. The †*Cerebropollenites* Province was characterized by high diversity of pteridophyte spores, together with spores of bryophytes and bisaccate and other gymnosperm pollen. Nonbisaccate pollen included †*Araucariacites*, †*Cerebropollenites* (“a common and distinctive element in the province”) (Herngreen et al., 1996: 1158), †*Classopollis*, and other gymnospermous pollen types. Angiosperm pollen made up only a small percentage of the assemblage (Herngreen & Chlonova, 1981; Srivastava, 1981, 1994; Herngreen et al., 1996).

However, Srivastava (1994) recognized an Early Cretaceous (Neocomian) Equatorial Province (a pre-Albian Early Cretaceous †*Dicheiropollis etruscus*/

†*Afropollis* Province in part), which was characterized by the gymnosperm †*Dicheiropollis*. According to Srivastava (1994), this province became differentiated from the southern and northern portions of the Boreal (†*Cerebropollenites*) and Austral (†*Microcachyridites*, a podocarp) Provinces, respectively, that represented continuities of these two phytoprovinces from the Jurassic. The southeastern United States was included in Srivastava’s (1994) Equatorial Province, and from his map it appears that Kentucky would be near the border between the Equatorial and Boreal Provinces. However, the southeastern United States was not included in the Equatorial Province as delineated by Herngreen et al. (1996), in which case Kentucky clearly is included in the Boreal (†*Cerebropollenites*) Province in the Early Cretaceous.

MIXED MESOPHYTIC FORESTS OF KENTUCKY AND CHINA

There are differences in both species composition and physiognomy between the eastern Asian and eastern North American Mixed Mesophytic Forest (Braun, 1950; Li, 1953; Wang, 1961; Wolfe, 1979). Thus, compared to the Mixed Mesophytic Forest of eastern North America, the Mixed Mesophytic Forest of eastern Asia has a higher woody species richness,

a higher number of primitive families of woody plants, a higher proportion of broad-leaved evergreen trees and shrubs, a higher percentage of woody taxa with entire-margined leaves, and a higher number of gymnosperm taxa. Based on Wolfe's (1979) classification system of humid to mesic forests of eastern Asia, the potential natural vegetation of most sites in Kentucky would be a Notophyllous (leaf sizes 20.25–45.00 cm²; see Dilcher, 1973) Broad-leaved Evergreen forest, as pointed out by Wolfe (1979: 27), for the deciduous forest of eastern North America in general. Wolfe states that, "...the bulk of the broad-leaved deciduous forests of eastern North America live under a mean annual temperature and a mean annual range of temperatures typical for broad-leaved evergreen forest regions and that fundamentally much of the broad-leaved deciduous forest of North America is an analog of the *secondary vegetation* [italics ours] of the Asian Notophyllous Broad-leaved Evergreen forest region."

Wolfe (1979) suggested that the lack of broad-leaved evergreen trees in the Eastern Deciduous Forest is due to intense cold waves from the Arctic (e.g., the polar vortex of January 2014), which penetrate this region unobstructed by the north-south-trending Appalachian Mountains. In China, on the other hand, cold waves originating in Siberia are blocked from reaching the Mixed Mesophytic Forest by east-west-trending mountains, which, however, have passes (gaps) that allowed migration of Mixed Mesophytic Forest taxa southward as the climate cooled. Thus, although mean annual temperature and mean annual range of temperatures in some parts of Kentucky are within the ranges of those that support Mixed Mesophytic Forest in China, absolute lows in Kentucky (and other parts of eastern North America) are lower than those in this similar forested region of Asia (Wolfe, 1975). According to Wolfe, differences in temperature parameters between the Mixed Mesophytic Forest regions of eastern North America and eastern Asia explain why broad-leaved evergreens are a significant part of this forest type in eastern Asia but are not an important component of the Mixed Mesophytic Forest in eastern North America. Wolfe's contention that there is a greater proportion of broad-leaved evergreen trees in the eastern Asian Mixed Mesophytic Forest than in the eastern North American Mixed Mesophytic Forest because of the extreme lower minimum temperatures in eastern North America is in agreement with the hypothesis of plant geographers/vegetation ecologists that "evergreenness versus deciduousness in extra-tropical forest climates is controlled by extreme minimum temperatures" (Box, 1995, 2002: 148).

Wolfe (1979, 1985) suggested that the broad-leaved deciduous forest of the southeastern United States developed in the Late Cenozoic (Miocene, ca. 13 Ma) from a broad-leaved evergreen forest with a subdominant deciduous component (e.g., *Carya*, *Fagus*, *Liquidambar*) that was dominant in the region in the mid-Cenozoic following the Eocene terminal event. Thus, the dominant broad-leaved evergreens were eliminated gradually from the region by the intense Arctic cold fronts that apparently developed in the Neogene. This scenario does not agree with the vegetation sequence outlined in Figure 2, which shows that a broad-leaved deciduous forest was present by the Oligocene.

Other factors that contribute to the greater species richness in the Mixed Mesophytic Forest of eastern Asia than in eastern North America are that this forest type in Asia (1) has been enriched progressively via migration of tropical and subtropical elements from south of it (whereas for geographical reasons this is not the case for the Mixed Mesophytic Forest of eastern North America), (2) was less extensively glaciated during the Quaternary, (3) is topographically (including elevation) more diverse, and (4) has been progressively enriched via diversification of lineages that already were present (Wolfe, 1977, 1979; Hsü, 1983; Latham & Ricklefs, 1993; Axelrod et al., 1996; Guo, 1999; Qian & Ricklefs, 2000; Ricklefs et al., 2004; Xiang et al., 2004; Renner et al., 2008). The ultimate source of some taxa in the rich woody flora of southern and eastern China may have been via infiltration of Gondwanan elements into it in the Tertiary/Pleistocene, as a result of the Australian plate moving north and coming into contact with the Eurasian plate (Florin, 1963; Schuster, 1972, 1976).

TIMES OF DISJUNCTIONS BETWEEN EASTERN ASIAN–EASTERN NORTH AMERICAN TAXA

The floristic similarities between eastern Asia and eastern North America involve tropical evergreen, temperate deciduous, and boreal and alpine taxa, and thus they could not be the result of a single historical event (Tiffney, 1985a; Xiang et al., 1998; Wen, 1999; Donoghue & Smith, 2004; Pennington & Dick, 2004). Instead, according to Tiffney, the disjunctions were established at several different times in the geologic past. Following is a summary of five historical patterns Tiffney suggests contributed to the floristic similarity between eastern North America and eastern Asia.

1. Late Cretaceous. Some of the disjunct taxa may have originated from the †*Aquilapollenites*–†*Normapolles* pollen provinces (see Muller, 1970; Meyen, 1987), e.g.,

Juglandales (Friis, 1983; Sims et al., 1999). Other groups that may have become established during this time include bryophytes, ferns, Pinaceae (but not *Pinus*), aquatics, and monocots.

2. Early and Middle Eocene. Basic components of the boreotropical flora evolved in the Paleogene, when a warm climate and land bridges between continents of the Northern Hemisphere allowed its spread (also see Tiffney & Manchester, 2001). Evergreen disjuncts such as Magnoliaceae, Theaceae, and Lauraceae may be accounted for here. Deciduous woody taxa and herbs of the forest floor as well as colonizers of disturbed sites may have accompanied the evergreens. However, some of the deciduous taxa may have moved later in the Tertiary (cooler climate) or evolved in parallel from ancestors inhabiting both areas. Winter darkness, not low temperatures, may have prevented broad-leaved evergreens from crossing the Bering land bridge, which was located at about 75°N paleolatitude. In which case, only deciduous taxa could have crossed it. On the other hand, both deciduous and evergreen taxa could have crossed the North Atlantic land bridge, which lay at a considerably lower latitude (ca. 55°N paleolatitude) than the Bering land bridge. As such, the North Atlantic land bridge was within the same climatic zone as that of Eocene floras, such as the London Clay (Chandler, 1964), with a tropical/subtropical floristic composition, and "... well south of the zone of extensive winter darkness" (Tiffney, 2000; Tiffney & Manchester, 2001: S9).
3. Late Eocene–Oligocene. Deciduous taxa of polar regions spread south. The North Atlantic land bridge was broken up in the Eocene (but see below). Taxa adapted to cooler climates may have moved via the Bering land bridge.
4. Miocene. The Bering land bridge was still present, but cool climate allowed passage of temperate plants only. The North Atlantic land bridge may have existed as a series of stepping stones (see below) and thus permitted passage of some temperate taxa. Some extant temperate taxa may have evolved in parallel from common ancestors in these two areas. Many disjunct herbaceous angiosperm groups evolved during this time, and these may have moved via the Bering land bridge by colonization of disturbed sites in existing forests and as components of open communities. Recent studies on the paleoflora and on the phylogeny and biogeography of several plant groups represented in the Miocene flora of Iceland offer strong support that the North Atlantic land bridge served as a physical link for migration of temperate woody plants between the Old World and the New World through the latest Miocene (Denk et al., 2005, 2010; Grimsson et al., 2007). In contrast to his earlier thinking, Tiffney (2008: 140) now believed that, "[t]he NALB [North Atlantic land bridge] may still have been functional in the later Neogene."
5. Late Tertiary–Quaternary. Arctic and alpine plants evolved and migrated across the Bering land bridge (also see Qian, 1993, 1999). Both molecular phylogenetic (Xiang et al., 1998, 2000; Wen, 1999; Xiang & Soltis, 2001) and fossil (Manchester, 1999) data support the hypothesis that eastern Asian and eastern North American disjunctions (1) represent relicts of a Mixed Mesophytic Forest that was distributed across the mid-latitudes of the Northern Hemisphere in the Miocene and, (2) as postulated by Tiffney (1985a), have multiple origins, i.e., movement of taxa occurred at different times and via different geographical routes. Most of the disjunct taxa appear to have diverged in the Neogene (Miocene–

Pliocene) (Wen, 1999; Xiang et al., 2000; Chanderbali et al., 2001; Donoghue et al., 2001; Liu et al., 2002; Donoghue & Smith, 2004; Nie et al., 2006, 2007, 2010; Jiao & Li, 2009). Manchester's (1999) finding that the circumboreal pattern of distribution of Asian, European, and North American genera was strongest in the Miocene offers strong support for hypothesis number one.

Further, although there are exceptions (e.g., Li, 2008; Jiao & Li, 2009; González et al., 2014), phylogenetic data have shown that most disjunctions involve closely related taxa, but not sister species, when more than two taxa are analyzed (Xiang et al., 1998, 2000; Wen, 1999; Fu et al., 2005; Zhou et al., 2006). Thus, phylogenetic analysis of closely related species with an eastern Asian–eastern North American–western North American disjunct pattern (e.g., *Trautvetteria caroliniensis* (Walter) Vail [Ranunculaceae] in eastern North America, *T. grandis* Nutt. in western North America, and *T. japonica* Siebold & Zucc. in eastern Asia; and *Calycanthus floridus* L. [Calycanthaceae] in eastern North America, *C. occidentalis* Hook. & Arn. in western North America, and *C. chinensis* W. C. Cheng & S. Y. Chang in eastern Asia) shows that the eastern and western North American species are more closely related to each other than either is to the eastern Asian species. That is, eastern and western North American species are sister groups, and the Asian species are the sister groups to the North American species (Xiang et al., 1998; also see Xiang & Soltis, 2001). This indicates that further divergence (geographical isolation) of taxa occurred after the initial disjunction in the Miocene–Pliocene. Thus, in contrast to fossil data, both the present-day disjunction pattern of sister taxa between eastern and western North America (Hong, 1993) and molecular phylogenetic data (Xiang et al., 1998; Wen, 1999; Fu et al., 2005; Harris & Xiang, 2009; Harris et al., 2009) support a strong biogeographic relationship between these two areas (Wen, 1999).

But did all Eurasian–North American disjunctions within genera originate via land bridges? What about long-distance dispersal via water, wind, birds, and floating islands? Although Milne (2006: 465) believes that land bridges are the more likely cause of these disjunctions, he does not rule out long-distance dispersal for "... explanations for disjunctions in any individual genus." Lavin and Luckow (1993) embraced the boreotropical hypothesis as explaining the occurrence of paleotropical taxa in North America during the Early Cenozoic and the subsequent migration of this tropical element to a refugium in seasonally dry tropical forests in the Caribbean Basin and to South America via the Panamanian Land Bridge during the Pliocene.

Based on several subsequent studies of Fabaceae, Lavin and colleagues continued to embellish the boreotropical hypothesis (Lavin, 1995; Luckow, 1995; Lavin & Sousa S., 1995; Lavin et al., 2000, 2001), and in the meantime they implicated Africa as a refugium for boreotropical flora (Lavin et al., 2000). However, their later studies showed that (1) legume diversity and endemism in the Caribbean Basin is of geologically recent origin and thus much younger than the tectonic events that were thought to be responsible for a relictual boreotropical flora in the Antilles, (2) some lineages in Central and South America are older than the closure of the Panamanian Isthmus (ca. 3 Ma), and (3) the ancestral area of some taxa in the Antilles is South America. In sum, through many studies, most of which were with legumes, they have concluded that the estimated age of divergence of legume clades that occur between continents separated by an ocean are younger than the tectonic events that supposedly were responsible for their vicariance (Lavin et al., 2004; Pennington et al., 2004; Lavin & Beyra Matos, 2008; Ireland et al., 2010).

Many studies, especially those based on molecular phylogenetics and age estimates, have concluded that long-distance dispersal (by water and wind currents, rather than by tectonic history/vicariance) would be the most likely explanation for many transcontinental taxa (e.g., Baum et al., 1998 [*Adansonia* L., Malvaceae]; Renner et al., 2000 [Atherospermataceae], 2001 [Melastomataceae], 2010 [Monimiaceae]; Renner & Meyer, 2001 [Melastomataceae, tribe Melastomeae]; Winkworth et al., 2002 [transoceanic dispersal to and from New Zealand of various families/genera/one tribe]; Schnabel et al., 2003 [*Gleditsia*, Fabaceae]; Givnish et al., 2004 [Bromeliaceae, Rapateaceae]; Pennington & Dick, 2004 [palaeotropical rainforest → Amazon lowland rainforest (20% of species immigrant lineages; most taxonomic similarity derived from transoceanic dispersal)]; Renner, 2004a [eight families, 10 genera; Melastomataceae, tribe Melastomeae], 2004b [Melastomataceae]; de Queiroz, 2005 [oceanic long-distance dispersal of many plant taxa]; Knapp et al., 2005 [*Nothofagus* Blume, Nothofagaceae]; Yuan et al., 2005 [*Exacum* L., Gentianaceae]; Crisp et al., 2009 [transoceanic colonizations contributed to biome (phylogenetic) stasis in the Southern Hemisphere]; Ickert-Bond et al., 2009 [*Ephedra* L., Ephedraceae]; Li et al., 2009 [*Bridelia* Willd., Phyllanthaceae]; Schaefer et al., 2009 [Cucurbitaceae]; Duchon & Renner, 2010 [*Cayaponia* Silva Manso, Cucurbitaceae]; Ireland et al., 2010 [*Ateleia* (DC.) Benth., Fabaceae]; Michalak et al., 2010 [Hernandiaceae]; Bartish et al., 2011 [Sapotaceae,

subfamily Chrysophylloideae]; Li et al., 2011 [*Persea* Mill. group, Lauraceae]; Kadereit & Baldwin, 2012 [long-dispersal may account for 10 (or 11, including *Anemone* L.) of 25 cases of disjunct distribution of plant taxa between western Eurasia and western North America]; Lambertini et al., 2012 [*Phragmites* Adans., Poaceae]; Rivadavia et al., 2012 [*Drosera* L., Droseraceae]; Crisp & Cook, 2013 [48% of 85 Australian vascular plant clades arrived to that continent by transoceanic dispersal]; Nie et al., 2013 [*Paederia* L., Rubiaceae]; Iles et al., 2014 [*Triethuria* Hook. f. (monogeneric family Hydatellaceae)]; Conran et al., 2014 [*Luzuriaga* Ruiz & Pav., Alstroemeriaceae, several transoceanic events across the Southern Ocean]; and Thomas et al., 2014 [Winteraceae]).

Li et al. (2011) explained the biogeography of the *Persea* group (Lauraceae) by a combination of vicariance (boreotropical hypothesis) and long-distance dispersal. The case for long-distance dispersal seems to be especially strong for trans-Atlantic dispersal of tropical genera between Africa and South America. Arrival of immigrants from Africa to South America and from South America to Africa occurred millions of years after the separation of the African and South American plates (ca. 105 Ma) and after land bridges were available for passage of plants across the tropical Atlantic (Morley, 2003; Renner, 2004a; Duchon & Renner, 2010). According to Raven and Axelrod (1974), exchange of plants between South America and Africa would not have occurred after about 84 Ma except by long-distance dispersal.

In any case, however, migration via the North Atlantic land bridge (boreotropical hypothesis) has been used in a number of recent studies to explain the disjunction of various tropical plant taxa between the Old World and the New World (Davis et al., 2002, 2004; Weeks et al., 2005; Zerega et al., 2005; Muellner et al., 2006; Smedmark & Anderberg, 2007; Merckx et al., 2008; Erkens et al., 2009). Interestingly, the study by Davis et al. (2004) also supported Chaney's claim that the source of the tropical element in the flora of North America was South America. According to Davis et al. (2004), the Malpighiaceae originated in South America in the latest Cretaceous (ca. 68 Ma), migrated via the Caribbean Basin to North America, and then to the Old World via the North Atlantic land bridge. Furthermore, flowering material of †*Eoglandulosa warmanensis* (Malpighiaceae), which has distinctive features of the New World members of this family, has been collected from the Middle Eocene Claiborne Formation (ca. 43 Ma) in the southeastern United States (Table 2).

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REVISION OF THE BRAZILIAN HEMISPHERIC OVARY CLADE OF *VELLOZIA* (VELLOZIACEAE) WITH THE NEW *V. RELIGIOSA*¹

Renato Mello-Silva² and
Denise Sasaki²

ABSTRACT

Species of the hemispheric ovary clade of the Velloziaceae are presented. The *Vellozia hemisphaerica* group is endemic to the Espinhaço Range in Bahia, Brazil, and is composed of the five species *Vellozia canelinha* Mello-Silva, *V. caudata* Mello-Silva, *V. hemisphaerica* Seub., *V. jolyi* L. B. Sm., and *V. religiosa* Mello-Silva & D. Sasaki. The group is a monophyletic assemblage supported by an ovary outline that is broader than long and other plastid and nuclear molecular characters, as well as non-molecular characters. Identification keys for the species group, their morphological and anatomical descriptions, as well as comments on the affinities of the species and character evolution based on previous cladistic analysis, geographical distribution, and conservation status are presented. A new species, *V. religiosa*, is described, and *V. burlemarxii* L. B. Sm. & Ayensu and *V. campanuloides* Mello-Silva are synonymized with *V. hemisphaerica* and *V. caudata*, respectively. Lectotypification of the name *V. hemisphaerica* is also provided.

Key words: Bahia, Brazil, IUCN Red List, *Vellozia*, Velloziaceae.

The first species of the hemispheric ovary group of Velloziaceae were placed together by Smith and Ayensu (1976), who described and put *Vellozia burlemarxii* L. B. Sm. & Ayensu near *V. hemisphaerica* Seub. in their identification key. Both species were characterized by a hemispheric ovary (Figs. 1G, 2E, 3C, D) and minor vascular bundles in leaf blades (Fig. 4A–E, G). Later, Menezes (1980) included *V. jolyi* L. B. Sm. within the group, formally described afterward by Smith (1985). More recently, *V. campanuloides* Mello-Silva, *V. canelinha* Mello-Silva, and *V. caudata* Mello-Silva were also associated with the group (Mello-Silva, 1993). In Mello-Silva (2005), *V. burlemarxii*, *V. caudata*, *V. hemisphaerica*, and *V. jolyi* formed a clade supported by a hemispheric ovary, i.e., an ovary outline that is broader than long. However, this clade had no internal resolution. *Vellozia religiosa* Mello-Silva & D. Sasaki, a new species, is now described herein, and the names *V. burlemarxii* and *V. campanuloides* are synonymized to *V. hemisphaerica* and *V. caudata*, respectively. According to results from Mello-Silva et al. (2011), these species, all from Espinhaço Range in Bahia, Brazil, emerge as a monophyletic group and the clade is supported, among other characters, by

the hemispheric ovary. Systematics of the group is presented, along with consideration of the results of cladistic analysis, identification keys, morphological and anatomical descriptions, relationships among species, evolution of selected characters, geographical distribution, and conservation status.

MATERIALS AND METHODS

Morphological and anatomical studies are based on dried and on dried and spirit collections, respectively. Anatomical descriptions, regarded as absolutely necessary for the systematics of the Velloziaceae (Mello-Silva, 1996), follow those of Mello-Silva (1990, 2000), Menezes (1971), and Smith and Ayensu (1976). The delimitation of species is based on the taxonomic species concept, in which a species is defined by an exclusive feature or a combination of them, in an attempt to substantiate a natural unit (Rieppel, 2007; Assis & Brigandt, 2009). Exsiccatae are deposited in listed herbaria, acronyms according to Thiers (2015, continuously updated). All cited specimens have been examined, except where indicated. Author names are abbreviated according to IPNI (<<http://www.ipni.org>>). Distribution maps are based on those from Instituto Brasileiro de Geografia e Estatística (1972)

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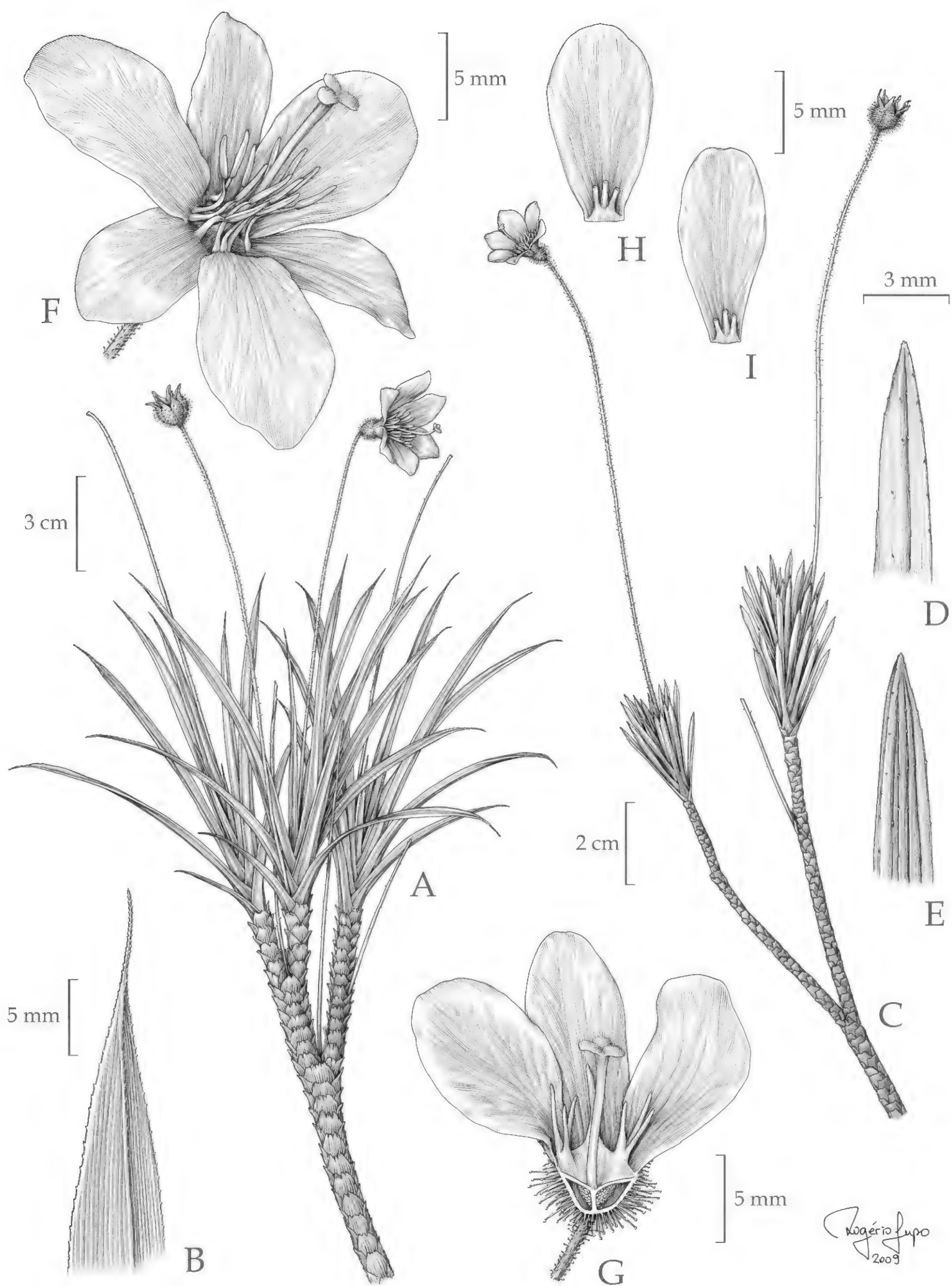


Figure 1. A, B. *Vellozia caudata* Mello-Silva. —A. Habit with flower and fruit. —B. Apex of lamina, abaxial side. C–I. *Vellozia religiosa* Mello-Silva & D. Sasaki. —C. Habit with flower and fruit. —D. Apex of lamina, abaxial side. —E. Apex of lamina, adaxial side. —F. Flower, showing 12 stamens. —G. Longitudinal section of flower with anthers removed, showing solitary stamen opposite to sepals and phalange of three stamens opposite to petals, and depressed obovoid hypanthium and ovary. —H, I. Petals, adaxial side, showing base of phalange of three stamens. A, B drawn from R. Mello-Silva 2565 (SPF); C–I, from B. L. Stannard H51864 (SPF).

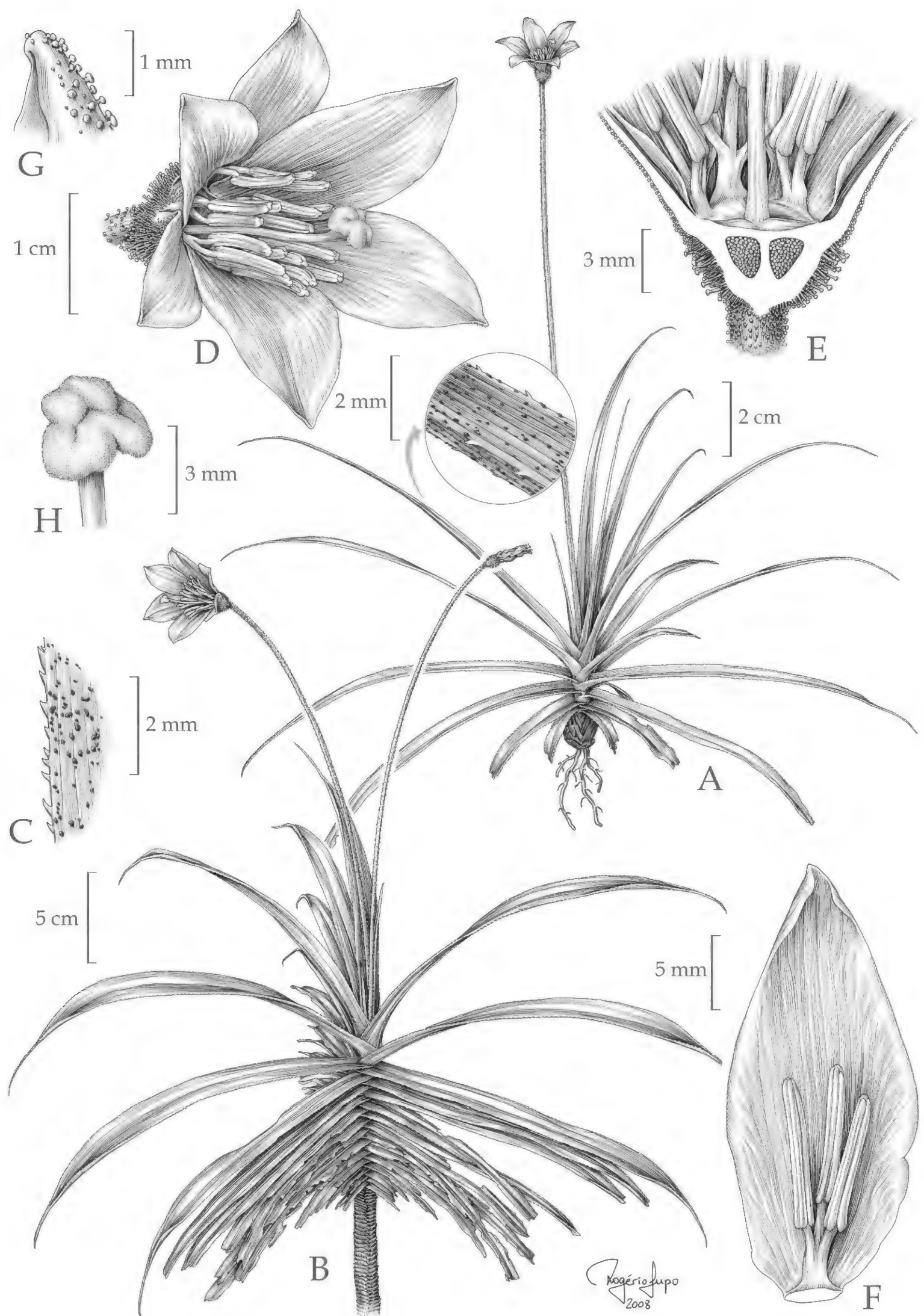


Figure 2. *Vellozia hemisphaerica* Seub. —A, B. Fertile habits with flower. —C. Detail of leaf margin, showing glandular-punctate adaxial surface and serrate margin. —D. Flower, showing 18 stamens. —E. Longitudinal section of proximal region of flower, showing phalanges of three stamens opposite to sepals and petals, and depressed obovoid hypanthium and ovary. —F. Petal, adaxial side, showing phalange of three stamens. —G. Sepal apex showing short glandular capitate-stipitate emergences on abaxial surface. —H. Apex of style with stigma. A is illustrated from R. Mello-Silva 2800 (SPF); B–H, from A. A. Conceição 184 (SPF).

and modified in ArcView (ESRI, 1999). Ink drawings are by Rogério Lupo.

THE HEMISPHERIC OVARY SPECIES GROUP IN CLADISTIC ANALYSES

Characters and cladistic support

In an initial cladistic analysis of morphological characters involving more than one species of the group (Mello-Silva, 2005), *Vellozia burlemarxii*, *V. caudata*, *V. hemisphaerica*, and *V. jolyi* emerged as a monophyletic assemblage, although without internal resolution. A hemispheric ovary (non-homoplastic within Velloziaceae), minor vascular bundles in the leaf blade, and a circular trilobate ovary were supporting synapomorphies.

In a second analysis with plastid and nuclear molecular characters, as well as morphological characters (Mello-Silva et al., 2011), nine terminals represented the hemispheric ovary group. The interrelationships from the consensus tree, (((*V. burlemarxii*, *V. campanuloides*, *V. caudata*, *Vellozia* aff. *caudata*, *V. hemisphaerica* 1, *V. hemisphaerica* 2) *V. canelinha*) (*V. jolyi*, *V. religiosa*)), were not well defined, but the group was supported by a non-homoplastic hemispheric ovary and by three homoplastic characters: specialized cells on the lamina surface (Fig. 3G), a circular, trilobate ovary, and poricidal capsules. Minor vascular bundles, which are smaller and situated above furrows, alternated with the normal ones in the leaf blade (cf. Fig. 4A–E, G), appear to have had a parallel evolution, both within and outside the clade. Within the hemispheric ovary group, they have appeared as a convergence in (*V. caudata*–*V. hemisphaerica*) and in *V. religiosa*, and outside the group in *V. plicata* Mart. from Brazil and *Xerophyta eglandulosa* H. Perrier from Africa. Each of the two main clades within the group ((*V. caudata*–*V. hemisphaerica*) *V. canelinha*) and (*V. jolyi*–*V. religiosa*) was supported by homoplastic synapomorphies. ((*Vellozia caudata*–*V. hemisphaerica*) *V. canelinha*) was supported by coronulate papillae in the furrows of the leaf blade (Fig. 4A–F) and (*V. jolyi*–*V. religiosa*) by spirotristichous phyllotaxis (Mello-Silva et al., 2011).

Autapomorphies of *Vellozia canelinha* are noteworthy. While it demonstrates an unusual habit within the group, with plants that grow up to 3 m, it has characters that are otherwise found in other significant clades within *Vellozia* Vand. These include fringed corona (Sajo et al., 2010) and ridged subsidiary cells in the stomata (Mello-Silva et al., 2011) as well as an aquiferous hypodermis extending only to bundle sheaths (cf. Fig. 4F, H, I), which characterizes both *V. canelinha* and *V. jolyi* and is

one of the characters that distinguishes the latter from its sister species, *V. religiosa*.

Eighteen stamens seem to be the basal condition in the genera (Menezes, 1980; Mello-Silva et al., 2011) and within the hemispheric ovary group. Within this group, 12 stamens could be a synapomorphy of the clade (*Vellozia jolyi*–*V. religiosa*) that has reverted to 18 in some populations of *V. jolyi*, or as a derived situation independently acquired by *V. religiosa* and some populations of *V. jolyi* (Mello-Silva et al., 2011). The dramatic increase in stamens in *V. canelinha*, up to 66, is remarkable, even among monocotyledons in general (Endress, 1995). This could suggest an apparent multiplication from an ancestor with 18 stamens, or it might indicate the existence of an extinct or yet unknown species with an intermediary number of stamens within the lineage of *V. canelinha*.

Internal relationships and synonymies

In Mello-Silva et al. (2011), the consensus of the total analyses revealed no definition among *Vellozia burlemarxii*, *V. hemisphaerica*, and *V. campanuloides*, *V. caudata*, or *Vellozia* aff. *caudata*. Nevertheless, the morphological analysis alone, although more unresolved as a whole, provided different information. *Vellozia burlemarxii* as sister to *V. hemisphaerica* has been supported by six character states, among them the absence of an abscission line between the sheath and lamina, which is exclusive within the group, and the triangular transverse section of the adult stem, a state shared only with *V. canelinha*, otherwise a quite distinct species. *Vellozia campanuloides*, *V. caudata*, and *Vellozia* aff. *caudata* share the same three character states (phyllotaxis tristichous, leaf blades arcuate, and presence of minor fibrovascular bundles); *V. caudata* and *Vellozia* aff. *caudata* additionally share revolute leaf blades, denoting their morphological resemblance. This evidence has been used here to maintain the submergence of these species and populations.

TAXONOMIC TREATMENT

1. ***Vellozia canelinha*** Mello-Silva, Kew Bull. 48: 5. 1993. TYPE: Brazil. Bahia: Rio de Contas, Pico das Almas, E slopes, Queiroz field, near track of Silvina farm, 13°32'S 41°57'W, 1500 m, 31 Oct. 1988, R. M. Harley 25810 (holotype, SPF!; isotypes, CEPEC!, E!, K!, MBM!, RB!, UEC!, US!).

Solitary, dracenoid plants; stems branched, (0.8–) 2–3 m, 5–9 mm diam. at apex. Leaves tristichous, 5 to 12 extant along apex of each branch; leaf sheaths brown, light brown at apex, glabrous, or sometimes

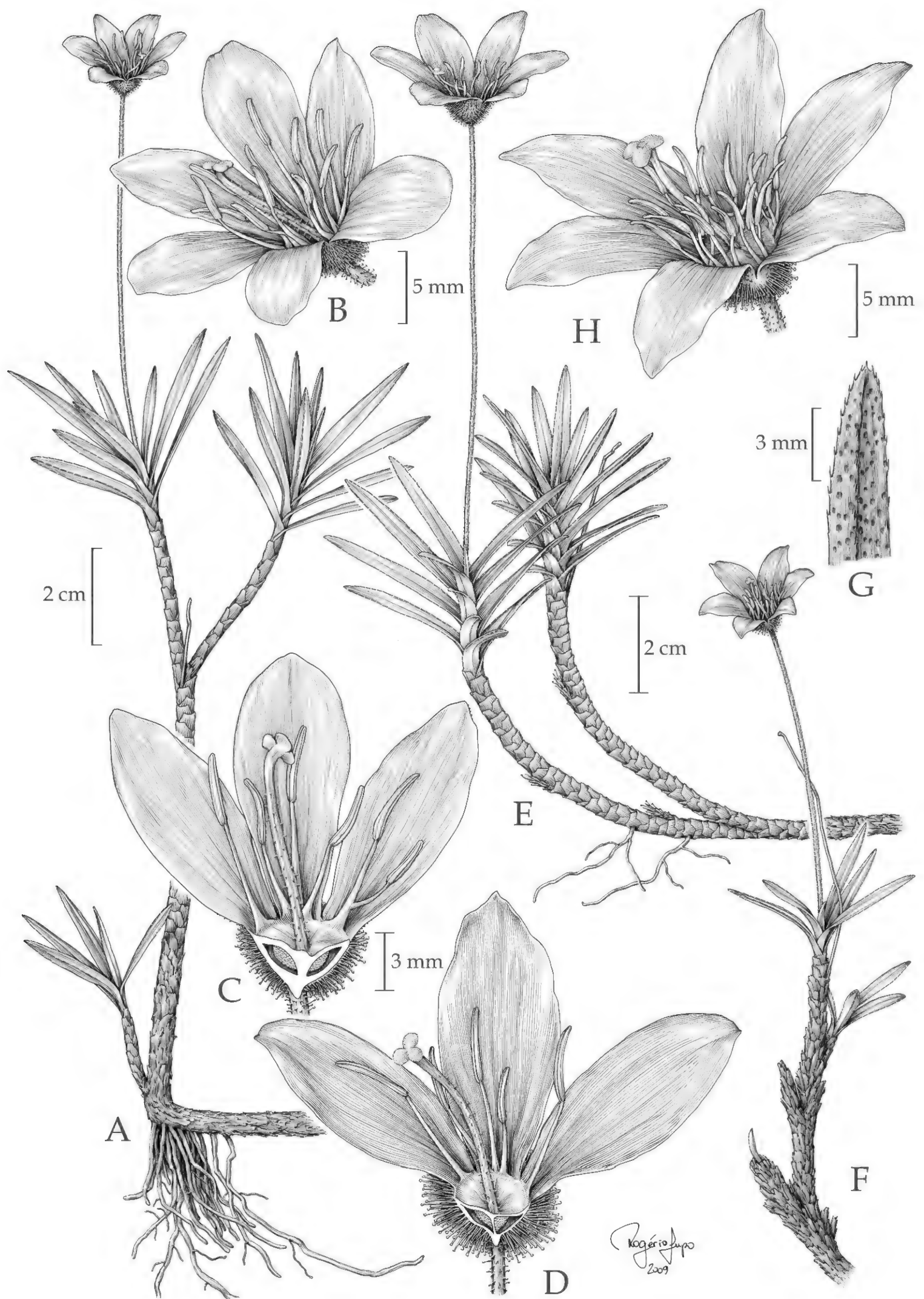


Figure 3. *Vellozia jolyi* L. B. Sm. —A, E, F. Fertile habits with flower. —B. Flower, showing 12 stamens. —C. Longitudinal section of flower showing solitary stamen opposite to one sepal, a phalange of two stamens opposite to another sepal and a phalange of three stamens opposite to a petal, and depressed obovoid hypanthium and ovary. —D. Longitudinal section of flower showing solitary stamen opposite to sepals and phalange of three stamens opposite to petals, and depressed obovoid hypanthium and ovary. —G. Leaf apex, showing glandular-punctate adaxial surface and serrate margins. —H. Flower, showing 18 stamens. A–D is drawn from A. M. Giulietti CFCR7092 (SPF); E, from R. Mello-Silva 2146 (SPF); F–H from A. A. Conceição 983 (SPF).

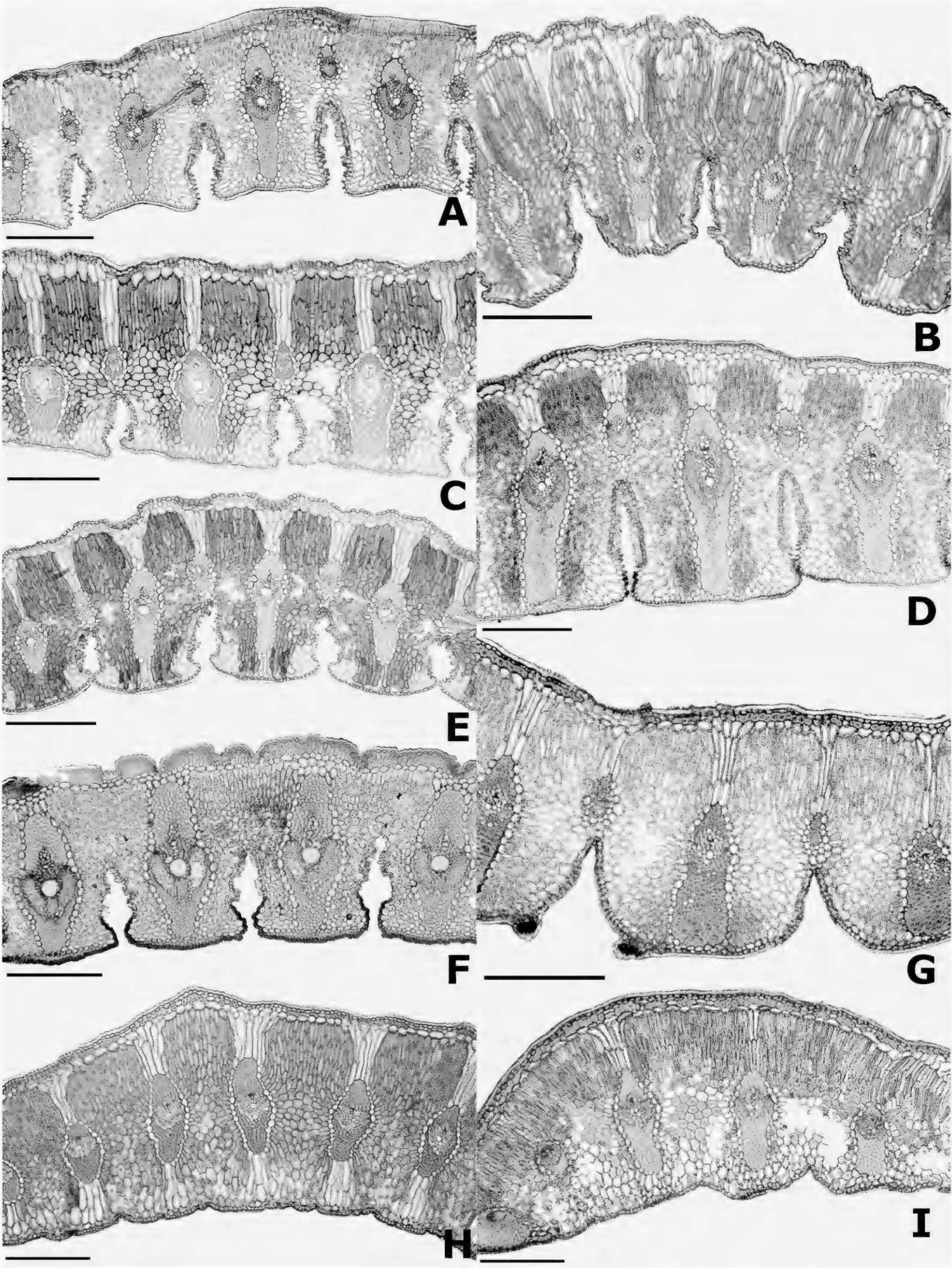


Figure 4. Cross section of median region of leaf blade. —A, C, D. *Vellozia caudata* Mello-Silva. —B, E. *Vellozia hemisphaerica* Seub. —F. *Vellozia canelinha* Mello-Silva. —G. *Vellozia religiosa* Mello-Silva & D. Sasaki. —H, I. *Vellozia jolyi* L. B. Sm. Scale bars = 200 μ m. (A from R. M. Harley 26521, SPF; B from F. França 2785, SPF; C from W. Ganey 1296, SPF; D from R. M. Harley 26700, SPF; E from A. A. Conceição 184, SPF; F from R. M. Harley 26570, SPF; G from R. M. Harley 20737, SPF; H from A. A. Conceição 187, SPF; I from K. Mori s.n., SPF 32977).

with emergences abaxially; leaf lamina 5.5–36 cm, 4–7 mm wide at base, linear-triangular, long attenuate, arcuate, revolute when dry, soon deciduous by abscission line, glabrous, adaxial surface densely glandular punctate, margins serrate or rarely entire, central nervature serrate on abaxial surface of proximal portion or sometimes along full length. Flowers 1 to 3 at each branch; pedicels 8–13 cm, purple, trigonous, laxly covered with glandular capitate-stipitate emergences. Hypanthium depressed-obovoid, circular-trigonous, 4–6 × 6–8 mm, densely covered with glandular capitate or stipitate, purple emergences, up to 3 mm; hypanthium tube absent; perianth oblong-elliptic to elliptic, violet; sepals 27–33 × 7–10 mm, petals ca. 25 × 1.2 mm; short glandular capitate-stipitate emergences laxly covering abaxial surface of sepals and proximal half of central nervature of petals; stamens 48 to 66, in phalanges of 8 to 11; filaments 6–8 mm, purple; anthers ca. 3 mm, yellow; corona violet; style ca. 20 mm, greenish; stigma ca. 1.5 mm diam., pale yellow. Capsule poricidal by apical slits on loculi, (3–)5–10 × 5–12 mm, hypanthium persistent; seeds ca. 0.7 mm, brown.

Leaf anatomy. Lamina dorsiventral; trichomes absent; cuticle thickened on adaxial surface; abaxial furrows ca. 1/3 thickness of lamina, coronulate-papillate; stomata confined to furrows; subsidiary cells ridged; specialized cells present on both surfaces; adaxial epidermis 3-seriate, sclerified except for short 2-seriate regions; abaxial epidermis 2-seriate, 1-seriate inside furrows; aquiferous 1-seriate hypodermis present on both surfaces, extending adaxially to bundle sheaths as aquiferous parenchyma; palisade mesophyll 4 cell-layers thick, adaxially merging with lacunar mesophyll; fibrovascular bundles of same type, surrounded by distinct bundle sheath; 1 large vessel present in each fibrovascular bundle; phloem strands 2, V-shaped, separated beneath xylem by fibers; fibers extending as girders, adaxially to aquiferous parenchyma and abaxially to hypodermis. Figure 4F.

Pedicel anatomy. Triangular in transverse section; fibrovascular bundles 8 to 12; belt of sclerified cells present.

Phenology. *Vellozia canelinha* has been collected in flower in October and November, and in fruit from January through March and in October.

Distribution. *Vellozia canelinha* is endemic to Rio de Contas region in Bahia and is particularly abundant in Pico das Almas slopes, in large

populations on rocky outcrops at elevations from 950 to 1500 m. Figure 5C.

IUCN Red List category. Although narrowly distributed, populations of *Vellozia canelinha* are extensive and occur over non-utilizable grounds. Thus, its conservation status is probably best described as Least Concern (LC), according to IUCN (2001) criteria.

Vernacular name and etymology. Canelinha, the Portuguese local name of the species, means small canela-d'ema, the vernacular name of several Velloziaceae for the resemblance of their stems to the skin pattern visible on the greater rhea's shin. The epithet is taken from the vernacular name, which is used as a noun in apposition.

Discussion. *Vellozia canelinha* is quite distinct from the other species of the group. The main differences are the dracenoid habit, with stems reaching 3 m tall, and the 48 to 66 stamens, which are among the highest numbers among the Velloziaceae and even among monocotyledons (Endress, 1995). The corona and ridged subsidiary cells in the stomata are also unique within the group, though present in one other clade of *Vellozia* (Mello-Silva et al., 2011). The absence of minor fibrovascular bundles is a probable reversion homoplastically shared with *V. jolyi* (Mello-Silva et al., 2011). The stems from *V. canelinha* are sold and used by local people to prepare decoctions that are said to be effective remedies for kidney and liver diseases (Mello-Silva, 1993).

Additional specimens examined. BRAZIL. **Bahia:** Rio de Contas, rd. to Fraga falls, Brumado river, 3 km of Rio de Contas, A. Furlan CFCR1675 (K, NY, SPF, UEC); Feb. 1987, J. R. Pirani s.n. (SPF 49381); track to Fraga falls, M. M. Silva 120 (HUEFS, SPF); rd. near Fraga falls, 13°35'56"S 41°49'36"W, R. Mello-Silva 2131 (K, SPF [2]); Pico das Almas, E slopes, SE of Queiroz, 13°32'S 41°58'W, R. M. Harley 26570 (CEPEC, F, K, R, SP, SPF, UB); Pico das Almas, Queiroz, near curral entrance, 13°31'02"S 41°57'00"W, R. Mello-Silva 2140 (HUEFS, K, SPF); ca. 8 km from city on rd. to Livramento do Brumado, V. C. Souza 5294 (K, SPF [2]).

2. *Vellozia caudata* Mello-Silva, Kew Bull. 48: 6. 1993. TYPE: Brazil. Bahia: Rio de Contas, Pico das Almas, E slopes, S of Queiroz, 13°32'S 41°57'W, 1500 m, 30 Nov. 1988, R. M. Harley 26521 (holotype, SPF!; isotypes, CEPEC!, E!, K!, MBM!, RB!, SP!, UB!, US!). Figure 1A, B.

Vellozia campanuloides Mello-Silva, Kew Bull. 48: 1. 1993, syn. nov. TYPE: Brazil. Bahia: Érico Cardoso (Água Quente), Pico das Almas, valley NW of Pico das Almas,

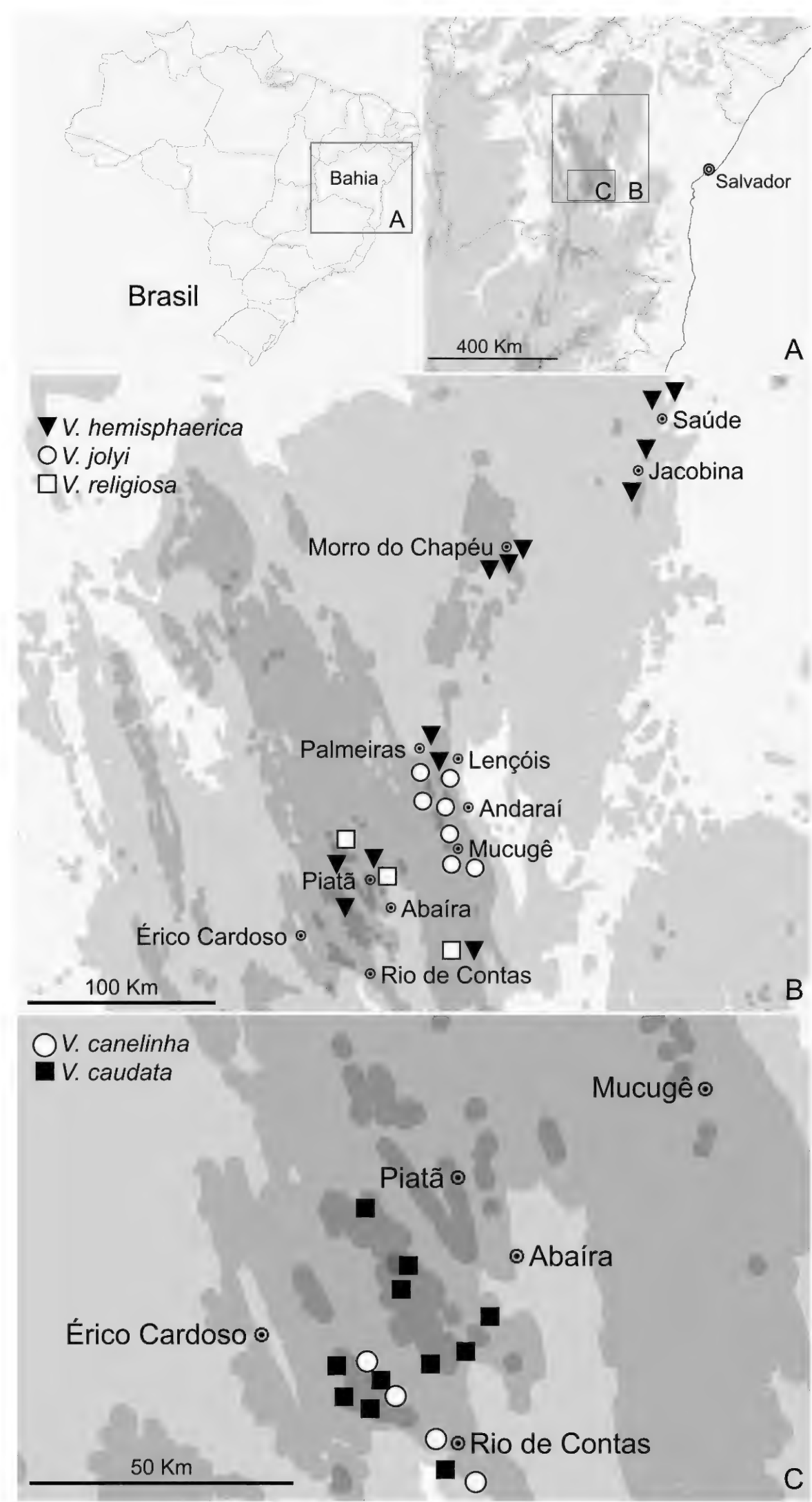


Figure 5. Distribution of the species in Brazil. —A. Espinhaço Range in Minas Gerais and Bahia States. —B. Espinhaço Range in Bahia. —C. Southern Espinhaço Range in Bahia. White: 0–500 m; light gray: 500–1000 m; medium gray: 1000–1500 m; dark gray: 1500–2000 m.

13°30'S 41°59'W, elev. 1450 m, 29 Nov. 1988, R. M. Harley 26700 (holotype, SPF!; isotypes, CEPEC!, K!, MBM!, RB!, SP!, US!).

Caespitose plants; stems branched, 3.5–35 cm, 2–14 mm diam. at apex. Leaves tristichous, 4 to 15 extant along apex of each branch; leaf sheaths brown, light brown to cinereous at apex, glabrous; leaf lamina 2–17 cm, 1–10 mm wide at base, linear-triangular, caudate to rarely long attenuate, arcuate, revolute when dry, rarely involute, soon deciduous by abscission line, glabrous, rarely with very sparsely disposed emergences abaxially, adaxial and sometimes abaxial surface densely glandular punctate, margins serrate, entire toward base, central nervature sometimes serrate toward apex on abaxial surface. Flower 1 at each branch; pedicels 2–21 cm, purplish, trigonous, laxly covered with glandular capitate-stipitate emergences. Hypanthium depressed ob-ovoid, circular to trigonous, 2–6 × 3–9 mm, light green to purplish green, densely covered with glandular capitate or stipitate, purple emergences, up to 4 mm; hypanthium tube absent; perianth oblong-elliptic to elliptic, purple; sepals 14–32 × 6–8 mm, petals 14–31 × 7–13 mm wide; short glandular capitate or stipitate emergences laxly covering abaxial surface of sepals and proximal half of central nervature of petals; stamens (16 to)18, in phalanges of 3; filaments 4–7 mm, purple to white; anthers 7–8 mm, yellow; corona absent; style 10–22 mm, greenish to yellowish white; stigma 3–4 mm diam., yellow. Capsule poricidal by apical slits on loculi, 2–8 × 3–13 mm, hypanthium persistent; seeds not seen.

Leaf anatomy. Lamina dorsiventral; trichomes absent; cuticle thickened on both surfaces; abaxial furrows ca. 1/2 thickness of lamina, coronulate-papillate; stomata confined to furrows, few present on abaxial surface; subsidiary cells smooth; specialized cells present on adaxial, rarely on abaxial, surface; adaxial epidermis 1- to 3-seriate, abaxial epidermis 1- or 2-seriate; aquiferous 1-seriate hypodermis present on both surfaces, extending adaxially to bundle sheaths as aquiferous parenchyma, and sometimes extending abaxially to inferior region of furrows; palisade mesophyll 3 or 4 cell-layers thick, adaxially merging with lacunar mesophyll; fibrovascular bundles of two types, smaller type radially arranged above furrows, both surrounded by a distinct bundle sheath; large vessels 1 to 3(4) present in each larger fibrovascular bundle, (0)1(2) in each smaller fibrovascular bundle; phloem strands 2, V-shaped, separated beneath xylem by fibers, or in smaller bundles separated by parenchyma or united beneath xylem; fibers extending as girders, adaxially

to aquiferous parenchyma and abaxially to hypodermis; bundles of subepidermal sclerified cells 1 or 2 cell-layers thick present beneath adaxial surface. Figure 4A, C, D.

Pedicel anatomy. Triangular in transverse section; fibrovascular bundles 6 to 12; belt of sclerified cells present.

Distribution. *Vellozia caudata* is endemic to Abaíra, Érico Cardoso (Água Quente), Rio de Contas, and the highest elevations of Chapada Diamantina, in Bahia, mostly at elevations from 1000 to 1900 m. It grows on large, horizontal, bare rocks, building up thickets of varying sizes (Mello-Silva, 1993) in places with sandy soil, or among rocks, on rocky soil. Figure 5C.

Phenology. *Vellozia caudata* flowers from October to April (to August), in the rainy season, and fruits throughout the year.

IUCN Red List category. There are many and numerous populations distributed over non-utilizable grounds. Thus, its conservation status is probably best described as Least Concern (LC), according to IUCN (2001) criteria.

Etymology. The epithet is derived from the caudate apices of the leaves.

Discussion. *Vellozia caudata* is similar to *V. jolyi* in habit and deciduous leaf blades. However, *V. caudata* has a tristichous phyllotaxis and arcuate leaf blades, with a caudate or attenuate apex, while *V. jolyi* has spirotristichous phyllotaxis and plane leaf blades, with a truncate apex. *Vellozia caudata* forms a clade with *V. hemisphaerica* that is supported, beyond the molecular transformations, by the presence of minor fibrovascular bundles in the leaf, and perhaps by the aquiferous hypodermis extending to bundle sheaths and furrows (Mello-Silva et al., 2011). On the other hand, the taxonomic differentiation of *V. caudata* from *V. campanuloides* (Mello-Silva, 1993) cannot be sustained. The characteristics that supposedly delimit *V. campanuloides*, the attenuate lamina and vessels in minor fibrovascular bundles, are also present in some populations of *V. caudata*. Another supposed autapomorphy, the involute leaves, could be due to the narrowness of the lamina of populations assigned to *V. campanuloides* (e.g., Harley 26700, Mello-Silva 2770). A similar phenomenon has been observed among populations of *V. hemisphaerica* and *V. hirsuta* Goethart & Henrard (Mello-Silva, 2011). Despite numerous collections of *V. caudata*, seeds have never been found.

Some populations of *Vellozia caudata* from Abaíra and Rio de Contas, in the localities of Arapiranga and Mato Grosso (*Ganev* 39, 173, 1296, 2078, *Mello-Silva* 2135, 2565, 2765), show individuals more robust, with longer and wider stems, and fibrovascular bundles in pedicels more numerous, although in a continuous variation from other populations of *V. caudata*. These populations were previously treated as *Vellozia* aff. *caudata* in Mello-Silva et al. (2011), where both emerge in a polytomy together with *V. burlemarxii* and *V. hemisphaerica*, both of these names also synonymized herein. Further resolution of the phylogenetic relationships within this polytomy will cast more light on the taxonomic position of these species.

Additional specimens examined. BRAZIL. **Bahia:** Abaíra, Bem Querer, 13°16'S 41°53'W, *R. M. Harley* H50348 (BHCB, CEN, HUEFS, K, MBM, SPF, UEC); Cigano, 13°15'S 41°55'W, *P. T. Sano* H52199 (CEPEC, HUEFS not seen, K, SPF); Catolés, Serra do Porco Gordo, Palmeira, 13°23'S 41°46'W, *W. Ganev* 173 (HUEFS, K, SPF); Catolés, Serra da Brenha, 13°18'S 41°53'W, *W. Ganev* 39 (HUEFS, K, SPF); Anáguas, above falls, 13°17'S 42°53'W, *W. Ganev* 1212 (HUEFS not seen, K, SPF); Serra das Brenhas, 13°19'S 41°53'W, *W. Ganev* 1296 (HUEFS, K, SPF); Catolés de Cima, Serra de Rei, track by Tijuquinho, 13°16'S 41°54'W, *W. Ganev* 1455 (HUEFS not seen, K, SPF); Serra dos Frios, 13°20'S 41°53'W, *W. Ganev* 2455 (HUEFS not seen, K, SPF); Serra de Rei, 13°17'S 41°54'W, *W. Ganev* 2778 (HUEFS not seen, K, SPF); Catolés, track to Barbado, A. A. *Conceição* 663 (SPF); Virassaia, 13°16'S 41°42'W, *Conceição* 675 (HUEFS not seen, SPF); Érico Cardoso (Água Quente), Pico das Almas, 17 km NW of Rio de Contas, S. A. *Mori* 13590 (CEPEC, NY not seen); Pico das Almas, W slopes, track to Santa Rosa, 23 km W of Érico Cardoso, 13°31'S 42°00'W, *R. M. Harley* 27059 (CEPEC, K, SPF); Pico das Almas, W slopes, betw. Paramirim das Crioulas & NNW face of peak, 13°31'S 42°00'W, *R. M. Harley* 27514 (CEPEC, K, SPF); Pico das Almas, W slopes, betw. Paramirim das Crioulas & NNW face of peak, 13°31'S 42°00'W, *R. M. Harley* 27534 (BHCB, CEPEC, K, MBM, SPF, US); Pico das Almas, valley ca. 5 km NNW from Queiroz, 13°30'13"S 41°58'18"W, *R. Mello-Silva* 2770 (SPF); Rio de Contas, Serra das Almas, *P. F. Lützelburg* 228 (M); Serra das Almas, *P. F. Lützelburg* 252 (M); NE slopes of Pico das Almas, ca. 25 km WNW from Rio de Contas, ca. 13°33'S 41°57'W, *R. M. Harley* 19681 (CEPEC, K, SPF); Pico das Almas, A. M. *Giulietti* CFCR6857 (HUEFS, K [2], MBM, MO, NY, PRE, R, SPF, U); Pico das Almas, *R. M. Harley* 24374 (K, SPF); slopes of Pico das Almas, *R. M. Harley* 24477 (CTES, K, MO, SPF, UB); Pico das Almas, E slopes, track Silvina farm–Queiroz, 13°32'S 41°56'W, *R. M. Harley* 26133 (CEPEC, K, SPF); Pico das Almas, E slopes, track to peak from Queiroz, 13°32'S 41°58'W, *R. M. Harley* 26426 (CEPEC, K, SPF); Pico das Almas, E slopes, track to peak from Queiroz, 13°32'S 41°58'W, *R. M. Harley* 26164 (CEPEC, K, SPF); Pico das Almas, E slopes, track to peak from Queiroz, 13°32'S 41°58'W, *R. M. Harley* 26165 (CEPEC, K, SPF); Pico das Almas, vertente leste, vale ao SE do Campo do Queiroz, 13°32'S 41°57'W, *R. M. Harley* 26530 (CEPEC, F, K, P, R, SP, SPF, UEC); Pico das Almas, E slopes,

Queiroz, 13°32'S 41°57'W, *R. M. Harley* 27300 (CEPEC, F, K, MBM, NY, RB, SPF); Água Suja river, 13°49'S 42°26'W, *W. Ganev* 2078 (HUEFS, K, SPF); Fraga falls, 13°35'59"S 41°49'72"W, *F. Juchum* 86 (CEPEC); Fraga falls, near rd., 13°35'56"S 41°49'36"W, *R. Mello-Silva* 2132 (HUEFS, K, SPF); Arapiranga, Água Suja river, right edge, 13°25'16"S 41°47'35"W, *R. Mello-Silva* 2135 (SPF); Pico das Almas, right of Queiroz, ca. 500 m beyond stream, 13°31'07"S 41°57'27"W, *R. Mello-Silva* 2139 (MBM, NY, SPF); Mato Grosso, 14 km from Brumado river dam to Mato Grosso, 13°28'31"S 41°51'10"W, *R. Mello-Silva* 2565 (SPF) [*idem*, *R. Mello-Silva* 2765 (SPF)].

3. *Vellozia hemisphaerica* Seub., Fl. Bras. (Martius) 3(1): 80. 1847. TYPE: Brazil. Bahia: Jacobina, Serra de Jacobina, 1837, *J. S. Blanchet* 2544 ([holotype, B not found] lectotype, designated here, G!; isoelectotypes, BM!, BR!, E!, K [2]!, LE [2]!, MO not seen, NY not seen, P [2]!). Figure 2A–H.

Vellozia burlemarxii L. B. Sm. & Ayensu, Smithsonian Contr. Bot. 30: 105. 1976, as “*burle-marxii*,” syn. nov. TYPE: Brazil. Bahia: Morro do Chapéu, Pedra de Chapéu, 14 Dec. 1968, *R. Burle Marx* s.n. (holotype, US not seen, digital image!).

Caespitose to solitary plants; stems branched to unbranched, 3.5–60 cm, 0.3–6 cm diam. at apex. Leaves tristichous, 5 to 13 extant along apex of each branch; leaf sheaths brown, glabrous, sometimes not exposed; leaf lamina 2–22 cm, 0.2–1.4 cm wide at base, linear-triangular, caudate or acuminate, arcuate, revolute when dry, sometimes involute, marcescent and reflexed when old, glabrous, adaxial surface densely glandular punctate, margins serrate, entire toward base. Flowers 1 to 4 at each branch; pedicels 5–27 cm, purplish to greenish purplish, trigonous, sparsely covered with glandular capitate or stipitate, green emergences. Hypanthium depressed obovoid, circular-trigonous, 3–7 × 4–7 mm, densely covered with glandular capitate or stipitate, deep purple to green emergences, up to 3 mm; hypanthium tube absent. Perianth oblong-elliptic to elliptic, purple or sometimes white; sepals 1.5–4.9 × 0.5–1.3 cm, petals 1.8–4.8 × 0.6–1.7 cm; short glandular capitate or stipitate emergences sparsely covering abaxial surface of sepals and proximal half, or rarely entire length, of central nervature of petals. Stamens 18, in phalanges of 3; filaments (2–)5–7 mm, white; anthers (4–)10–13 mm, yellow; corona absent; styles 15–32 mm, white to yellow; stigma 3–5 mm diam., yellow. Capsule poricidal by apical slits on loculi, 0.5–2 × 0.8–1.5 cm; hypanthium persistent; seeds 0.6–0.7 mm, brown.

Leaf anatomy. Lamina dorsiventral; trichomes absent; cuticle thickened on both surfaces; abaxial

furrows ca. 1/3 to 1/2 thickness of lamina, coronulate-papillate; stomata confined to furrows, few present on abaxial surface; subsidiary cells smooth; specialized cells present on adaxial and sometimes on abaxial surfaces; adaxial epidermis 1- to 3-seriate, abaxial epidermis 1-seriate; aquiferous 1- or 2-seriate hypodermis present on both surfaces, extending adaxially and abaxially to bundle sheaths as aquiferous parenchyma; palisade mesophyll 3 or 4 cell-layers thick, adaxially merging with lacunar mesophyll; fibrovascular bundles of two types, smaller radially arranged above furrows, both surrounded by a distinct bundle sheath; large vessels 1 or 2(3) present in each larger fibrovascular bundle, 1 to 3 in each smaller fibrovascular bundle; phloem strands 2, V-shaped, separated beneath xylem by fibers or in smaller bundles separated by parenchyma or united beneath xylem; fibers extending as girders, adaxially and abaxially to aquiferous parenchyma; bundles of subepidermal sclerified cells 1 or 2 cell-layers thick present beneath adaxial surface. Figure 4B, E.

Pedicel anatomy. Triangular in transverse section; fibrovascular bundles 6 to 14; belt of sclerified cells present.

Distribution. *Vellozia hemisphaerica* is relatively widely distributed from Abaíra to Saúde, along almost all the Espinhaço chain in the state of Bahia. The small to medium-sized populations grow on rocky outcrops, either in rocky furrows or over rock, generally in wet places or near streams, at elevations from 600 to 1700 m. Figure 5B.

Phenology. *Vellozia hemisphaerica* has been found in flower in every month except July, and in fruit throughout the year.

IUCN Red List category. *Vellozia hemisphaerica* is the most widely distributed species of the group, occurring throughout a large region, over non-utilizable grounds, with populations more or less extensive. Thus, its conservation status is probably best described as Least Concern (LC), according to IUCN (2001) criteria.

Etymology. The species is named after the striking hemispheric shape of the ovary and constitutes the diagnostic morphological synapomorphy of the group.

Discussion. The majority of populations of *Vellozia hemisphaerica* show a habit similar to that depicted in Figure 2B. Nevertheless, some populations from sandy places at Três Morros, municipality

of Piatã, show a much more delicate habit (Fig. 2A). The populations from Morro do Chapéu, until now classified as *V. burlemarxii*, show individuals less robust with leaf blades narrower and involute when dry, the latter character state shared with populations from Piatã (e.g., *Mello-Silva CFCR7414*, 2800) and with several collections of *V. caudata* with narrow leaf blades (Mello-Silva et al., 2011). There are always six fibrovascular bundles in the pedicels from the populations found in Morro do Chapéu; this number varies from six to 14 in other populations. The perianth of *V. hemisphaerica* is generally purple but, as in other species of *Vellozia* and *Xerophyta* Juss. (Ayensu, 1973; Mello-Silva, 2000, 2005, 2011; Mello-Silva et al., 2011), a white perianth can be found in some individuals.

In Mello-Silva et al. (2011), the two accessions representing *Vellozia hemisphaerica* in cladistics analyses fail to resolve as a supported clade, except in the morphological analysis, where they emerge as sister to *V. burlemarxii*, with this name here considered a synonym. Those results from molecular and combined analyses are paradoxical, as *V. hemisphaerica* is quite distinct from the other species of the group, e.g., in not showing an abscission line between sheath and lamina, the leaf thus being marcescent, and in having the xerophytic type of sclerenchyma pattern. These attributes are shared with *V. burlemarxii*, herein synonymized.

The chosen lectotype for *Vellozia hemisphaerica* is from the original collections at G gathered by Blanchet in Brazil, during his long tenure in Bahia as Swiss consul (Urban, 1896).

Additional specimens examined. BRAZIL. **Bahia:** Abaíra, Ouro Fino, 13°15'S 41°54'W, *B. L. Stannard H52149* (CEPEC, HUEFS, K, MBM, SP, SPF); Barra da Estiva, rd. to Capão da Volta & Jussape, Serra dos Três Capões, 12 km of Barra da Estiva & 7 km from Km. 177 of Barra da Estiva–Mucugê rd., 13°35'03"S 41°23'06"W, *R. Mello-Silva 2141* (SPF); Ibicoara, Serra do Sincorá, 13°23'S 41°13'W, *M. A. Nóbrega 351* (SPF); Jacobina, Morro do Cruzeiro, 11°11'22"S 40°30'29"W, *F. França 2448* (HUEFS not seen, SPF); N of Serra do Ouro hotel, 11°10'16"S 40°30'32"W, *R. Mello-Silva 2828* (SPF); Lençóis, Mucujezinho river, near Poço do Diabo, *A. A. Conceição 184* (HUEFS, SPF); Morro do Chapéu, Ferro Doido river, ca. 18 km E of Morro do Chapéu, *H. S. Irwin 32520* (C, F, IAN not seen, K, NY not seen); Agreste river, *G. G. Hatschbach 39691* (BR, C, MBM, SPF); 19.5 km of the town of Morro do Chapéu on the rd. (BA 052) to Mundo Novo, Ferro Doido river, 41°02'W 11°38'S, *R. M. Harley 19287* (CEPEC, K, RB, SPF); *N. L. Menezes CFCR379* (K [3], SPF); rd. Morro do Chapéu–Jacobina, 11°28'58"S 41°05'04"W, *A. M. Giuliatti PCD3255* (ALCB not seen, CEPEC not seen, HRB, HUEFS not seen, K not seen, SPF); 1 km SE from Morro do Chapéu on rd. to Mundo Novo, 11°33'32"S 41°08'48"W, *R. Mello-Silva 2148* (SPF); ca. 7 km E of Morro do Chapéu, 11°34'24"S 41°06'28"W, *F.*

França 4030 (HUEFS not seen, SPF); BR 052, vic. of bridge over Ferro Doido river, ca. 18 km E of Morro do Chapéu, S. A. *Mori 14507* (CEPEC, K, NY, SPF); near Ferro Doido falls, L. P. *Felix 7540* (IPA); Ferro Doido river, 22 km E of Morro do Chapéu, 11°37'36"S 41°00'07"W, F. *França 2785* (HUEFS not seen, SPF); Ferro Doido falls, 11°37'41"S 41°12'03"W, C. *Correia 124* (HUEFS); Ferro Doido river, 18 km SE from Morro do Chapéu on rd. to Mundo Novo, 11°37'33"S 41°00'15"W, R. *Mello-Silva 2149* (SPF); cultivated at Burle Marx's estate, N. L. *Menezes 399* (SPF); N. L. *Menezes 653* (SPF); s.d., R. *Burle Marx s.n.* (RB 160609); cultivated at Univ. São Paulo, N. L. *Menezes 1162* (SPF); Palmeiras, Pai Inácio, BR 242, Km. 232, ca. 15 km NE of Palmeiras, S. A. *Mori 12916* (CEPEC, NY not seen); Morro do Pai Inácio, 12°27'45"S 41°38'15"W, L. P. *Queiroz 1999* (HUEFS not seen, SPF); Morro do Pai Inácio, entre 12°27'25"S 41°28'40"W e 12°27'19"S 41°28'24"W, V. C. *Souza 5230/CFCR15541* (K, SPF); Pai Inácio, 12°27'20"S 41°28'15"W, A. M. *Carvalho PDC975* (ALCB, CEPEC, HUEFS not seen, K, SPF); Pai Inácio, Platô da Cruz, A. A. *Conceição 113* (SPF); Morro do Pai Inácio, along BR-242, 12°27'37"S 41°28'40"W, M. *Alves EBNN1018* (UFP); Piatã, Serra do Gentio, betw. Piatã & Serra da Tromba, R. *Mello-Silva et al. CFCR7414* (SPF); Serra da Tromba, rd. Piatã to "gerais da serra," via soccer field, 13°08'S 41°50'W, W. *Ganev 951* (HUEFS not seen, K, MBM, SPF); Serra de Santana, track to Capela do Senhor do Bonfim chapel, immediately E of Piatã, 13°09'04"S 41°45'54"W, R. *Mello-Silva 2576* (SPF); Morro dos Três Morros, Serra do Gentio, São Bartolomeu ("Bertolameu"), NNW base of Morro do Navio, 9.3 km N of Piatã on rd. Piatã-Boninal (BA 148) and 7.1 km W on vicinal rd. to Inúbia, 6.8 km NNW from that rd., 13°02'04"S 41°54'14"W, R. *Mello-Silva 2800* (SPF [2]); Pindobaçu, rd. from Carnaíba to Itapicuru, margins of Itapicuru river, cultivated at Univ. São Paulo, N. L. *Menezes 1303* (SPF); Saúde, rd. to Paiaió falls, 10°54'02"S 40°26'55"W, M. L. *Guedes PDC2903* (CEPEC).

4. **Vellozia jolyi** L. B. Sm., *Bradea* 4: 133. 1985. TYPE: Brazil. Bahia: Mucugê, Capa Bode Mtns., Andaraí-Mucugê rd., 1000 m, 2 Nov. 1973, A. B. *Joly s.n.* & N. L. *Menezes 316* (holotype, SP!; isotype, SPF!). [cf. "without exact locality," Smith, 1985: 133.] Figure 3A–H.

Caespitose plants; stems branched or not, 3–35 cm, 2–6 mm diam. at apex. Leaves spirotristichous, 5 to 27 extant along apex of each branch; leaf sheaths brown, light brown to cinereous at apex, glabrous, sometimes with emergences abaxially toward apex; leaf lamina 1–6.5 cm, 1.5–4 mm wide at base, linear-triangular, abruptly acute, plane, revolute when dry, soon deciduous by abscission line, glabrous, adaxial surface densely glandular punctate, margins serrate, sometimes entire. Flower 1 at each branch; pedicel 4.5–14 cm, purplish green, trigonous, sparsely covered with glandular capitate or stipitate emergences. Hypanthium depressed obovoid, circular to trigonous, (1–)2–5 × 1.5–6 mm, purplish green to green, densely covered with glandular capitate or stipitate purple emergences, up to 4 mm; hypanthium

tube absent; perianth oblong-elliptic to elliptic, purple, purplish blue, pinkish, or white; sepals 12–25 × 5–8 mm, petals 12–23 × 6–9 mm; short glandular capitate or stipitate emergences laxly covering abaxial surface of sepals and proximal half of central nervature of petals; stamens 12 to 18, either 3 opposite to sepals and 9 to petals, in phalanges of 3, or all in phalanges of 3, with the lateral 2 smaller than central; filaments 2–6 mm, purple to white; anthers 3–7 mm, yellow; corona absent; styles ca. (10–)13–17 mm, white; stigma 1.5–3 mm diam., yellow. Capsule poricidal by apical slits on the loculi, 3–5(–10) × ca. 10 mm, hypanthium persistent; seeds 0.7–1 mm, brown.

Leaf anatomy. Lamina dorsiventral; trichomes absent; cuticle not thickened or thickened on adaxial surface or on both surfaces; abaxial furrows ca. 1/4 thickness of lamina, sometimes absent, papillae inconspicuous or absent; stomata confined to furrows or to region between 2 fibrovascular bundles on abaxial surface when furrows absent; subsidiary cells smooth; specialized cells present on adaxial, rarely on abaxial, surface; adaxial and abaxial epidermis 1- to 2-seriate; aquiferous 1- to 2-seriate hypodermis present on both surfaces, extending adaxially, and sometimes abaxially, to bundle sheaths as aquiferous parenchyma; palisade mesophyll 3 or 4 cell-layers thick, adaxially merging with lacunar mesophyll; fibrovascular bundles of one type, surrounded by a distinct bundle sheath; large vessels 1 to 3 present in each fibrovascular bundle; phloem strands 2, V- or U-shaped, separated beneath xylem by fibers and parenchyma; fibers extending as girders, adaxially to aquiferous parenchyma and abaxially to hypodermis or to aquiferous parenchyma; bundles of subepidermal sclerified cells 1 or 2 cell-layers thick present beneath both surfaces. Figure 4H, I.

Pedicel anatomy. Triangular in transverse section; fibrovascular bundles 6; belt of sclerified cells present.

Distribution. *Vellozia jolyi* is endemic to the middle portion of the Espinhaço chain in Bahia, from Mucugê to Lençóis, where the highest concentrations and dense populations grow on flat, rocky outcrops, at elevations from 800 to 1500 m. Figure 5B.

Phenology. *Vellozia jolyi* flowers and fruits throughout the year.

IUCN Red List category. *Vellozia jolyi* is distributed over a relatively extended region, with dense and localized populations over non-utilizable grounds.

Thus, its conservation status is probably best described as Least Concern (LC), according to IUCN (2001) criteria.

Etymology. The species is named after Aylthon Brandão Joly, who initiated studies on phanerogamic systematics at University of São Paulo, Brazil, especially on campos rupestres vegetation, which comprises the habitat of the majority of the Velloziaceae.

Discussion. In cladistics analyses *Vellozia jolyi* has been sister to *V. religiosa*, and they share the apomorphies of a spirotristichous phyllotaxis, the distal portion of leaf blade truncate, and flowers always solitary (Mello-Silva et al., 2011). *Vellozia jolyi* can be differentiated from *V. religiosa* by the absence of minor fibrovascular bundles in its leaves, which are wider, more patent, and not mucronate. Northern populations of *V. jolyi*, from Guiné, in Mucugê, to Lençóis (e.g., *Conceição* 983, *Mello-Silva CFCR7161*), are composed of more robust plants without leaf furrows (Figs. 3E, 4H) and generally with 18 stamens, although this can vary from 12 to 18, as in *Mello-Silva* 2146 and *Conceição* 968, whose flowers bear 12, 15, or 18, and 15 to 18 stamens, respectively. The irregular number of stamens is due to the sporadic occurrence of extra stamens or their suppression in flowers (Fig. 3C). Southern populations, such as the type material from Serra do Capa Bode in Mucugê (Fig. 3A–D), are composed of less robust individuals. These always bear 12 stamens, and the furrows in the leaf blades may or may not be present (Fig. 4I). Plasticity in stamen number and in furrows is not an uncommon feature within some groups of *Vellozia* (Mello-Silva, 1990, 1995, 2000). Nevertheless, two stamens opposite to each tepal, as depicted by Smith (1985) when describing *V. jolyi*, was an erroneous representation. Perianth color in *V. jolyi* varies from purple, which is more common, to almost white.

Additional specimens examined. BRAZIL. **Bahia:** Andaraí, margins of Apiaba river, 22 Apr. 1981, *C. T. Rizzini* s.n. (SPF 32952); Apiaba river, *G. G. Hatschbach* 48225 (BR, C, CEPEC, HRB, K, MBM not seen, SPF); Igatu, Gruta do Brejão, *J. G. Jardim* 2320 (CEPEC not seen, SPF); Lençóis, Serra dos Lençóis, Serra Larguinha, ca. 2 km NE of Caeté-Açu (Capão Grande), 12°36'S 41°29'W, *R. M. Harley* 22573 (CEPEC not seen, K not seen, SPF); Serra Larga (Serra Larguinha), W of Lençóis, near Caeté-Açu, 12°36'S 41°29'W, *R. Mello-Silva CFCR7161* (K, MBM, SP, SPF); Serra Larguinha, W of Capão, *R. Kral* 72801 (SP, SPF); Serra Larga, July 1985, *C. A. M. Scaramuzza* s.n. (SPF 39881); Fumaça falls, *A. A. Conceição* 187 (SPF); near Fumaça falls, *A. A. Conceição* 617 (SPF); on track to Fumaça falls, *A. A. Conceição* 968 (SPF); Serra Larguinha, on top of hill on track to Fumaça falls, 12°36'07"S

41°28'41"W, *R. Mello-Silva* 2146 (SPF); Mucugê, Serra do Capa Bode, Nov. 1973, *G. C. P. Pinto* s.n. (ALCB 954, HRB); Serra do Arenito, 11 Mar. 1974, *D. Andrade-Lima* s.n. (F, MBM, NY, R, RB, SPF 32846, U, UB, US); Serra do Sincorá, 7 km N of Mucugê on rd. to Andaraí, *C. E. Calderón* 2424 (CEPEC, K, SPF, US not seen); rio Cumbica, ca. 3 km N of Mucugê on rd. to Andaraí, 12°59'S 41°21'W, *R. M. Harley* 18699 (CEPEC not seen, K, SPF); rd. Andaraí–Mucugê, 3 Apr. 1977, *K. Mori* s.n. (SPF 32977); 10–12 km NW of Mucugê, on rd. to Andaraí, 12°57'S 41°20'W, *S. A. Mori* 12665 (CEPEC, NY not seen, US not seen); ca. 2 km on rd. to Andaraí, 12°59'S 41°21'W, *R. M. Harley* 20580 (CEPEC, F, IPA, K [2], MBM, MO, NY, PRE, R, RB, SP, SPF, U, UEC, US); near Mucugê, 12°58'58"S 41°21'07"W, *A. P. Araújo* 292 (HRB, SPF); *N. L. Menezes* 1014 (IPA, K, MBM, MO, RB, SPF, U); main valley N of Mucugê from 3 to 8 km N of town, *R. M. King* 8733 (K, US not seen); *N. L. Menezes* 1154 (K, SPF); rd. Andaraí–Mucugê, *A. M. Giulietti CFCR7092* (K, SPF); rd. Andaraí–Mucugê, 27 km S of Andaraí, beyond Piaba river, *M. G. L. Wanderley* 941 (SP, SPF); rd. Andaraí–Mucugê, 27 km S of Andaraí, near cross of Piaba river, *M. G. L. Wanderley* 949 (SP, SPF); near town, *G. G. Hatschbach* 50090 (BR, C, HRB, HUA, K, MBM not seen, SPF); beyond Cumbuca river, 12°18'S 41°19'W, *J. S. Assis* 424 (HRB); rd. to Andaraí, Km. 28, bridge over Piaba river, 12°57'S 41°16'W, *M. Luceño EBNN317* (UFP); rd. Andaraí–Mucugê, near Embratel tower, 12°57'26"S 41°19'14"W, *D. J. N. Hind PCD3547* (ALCB not seen, CEPEC not seen, HRB, HUEFS not seen, K, SPF); Pedra Redonda, betw. Preto & Paraguaçu rivers, 21°57'00"S 41°24'27"W, *R. M. Harley PCD3642* (ALCB, CEPEC, HUEFS not seen, K, SPF); near confluence of Mucugê & Cumbuca rivers, *H. P. Bautista UMS74* (HRB); 8 km of Mucugê on rd. to Andaraí, near Embratel tower, *H. P. Bautista* 2942 (HRB [2]); Guiné, *A. A. Conceição* 714 (SPF); Guiné, *Conceição* 901 (SPF); Guiné, Serra do Esbarrancado, *A. A. Conceição* 956 (SPF); Guiné, Serra do Esbarrancado, *A. A. Conceição* 983 (SPF); Mpio. park, 12°59'18"S 41°20'27"W, 25 Jan. 2003, *N. Roque* s.n. (ALCB 61399 not seen, SPF); rd. Mucugê–Andaraí, 8.9 km of Mucugê, near TV tower, 12°57'30"S 41°19'15"W, *R. Mello-Silva* 2145 (SPF); slopes of Serra da Tesoura, 13°07'50"S 41°20'53"W, *E. L. Borba* 1888 (HUEFS not seen, SPF); Pico do Gobira, 13°04'36"S 41°22'40"W, *E. B. Souza* 1017 (HUEFS, SPF); cultivated at Roberto Burle Marx's estate, *N. L. Menezes* 451 (SPF).

5. *Vellozia religiosa* Mello-Silva & D. Sasaki, sp. nov. TYPE: Brazil. Bahia: Piatã, Três Morros, 13°04'S 41°54'W, 1400 m, 10 Mar. 1992, *B. L. Stannard* H51864 (holotype, SPF!; isotypes, CEPEC not seen, HUEFS not seen, K!). Figure 1C–I.

Foliis spiraliter trifariis apicem versus abrupte acutis atque floribus semper solitariis *Velloziae jolyi* L. B. Sm. appropinquat, sed ab ea foliis mucronatis minus patentibus nervis minoribus supra sulcos instructis differt.

Caespitose plants; stems with no to few branches, 10.5–18 cm, ca. 3 mm diam. at apex. Leaves spirotristichous, 5 to 16 extant along apex of each branch; leaf sheaths brown, cinereous at apex, glabrous, often with emergences; leaf lamina 1.3–

2.5 cm, 1–2 mm wide at base, linear-triangular, abruptly acute, mucronate, plane, involute when dry, soon deciduous by abscission line, sparsely disposed emergences on distal half of abaxial surface and sometimes on adaxial surface, otherwise glabrous, adaxial surface densely glandular punctate, margins entire, sometimes obscurely serrate. Flower 1 at each branch; pedicel ca. 5.5 cm, purplish green to green, trigonous, sparsely covered with glandular capitate or stipitate emergences. Hypanthium depressed obovoid, circular-trigonous, ca. 2×4 mm, purplish green to green, densely covered with glandular capitate or stipitate emergences, up to 2 mm; hypanthium tube absent; perianth oblong to elliptic, purple; sepals ca. 10×5 mm, petals ca. 12×6 mm; short glandular capitate or stipitate emergences laxly covering abaxial surface of sepals and proximal half of central nervature of petals; stamens 12, three opposite to sepals, 9 opposite to petals, in phalanges of 3, with lateral 2 smaller than central; filaments ca. 8 mm, purple to white; anthers ca. 5 mm, yellow; corona absent; style ca. 16 mm, white; stigma 0.5 mm diam., yellow. Capsule poricidal by apical slits on loculi, ca. 3×6 mm, hypanthium persistent; seeds ca. 1 mm, brown.

Leaf anatomy. Lamina dorsiventral; trichomes absent; cuticle thickened on both surfaces; abaxial furrows ca. 1/3 thickness of lamina, papillae absent; stomata confined to furrows, few present on abaxial surface; subsidiary cells smooth; specialized cells present on both surfaces; adaxial and abaxial epidermis 1- or 2-seriate; aquiferous 1-seriate hypodermis present on adaxial surface, extending adaxially to bundle sheaths as aquiferous parenchyma; palisade mesophyll 4 cell-layers thick, adaxially merging with lacunar mesophyll; fibrovascular bundles of two types, smaller radially arranged above furrows, both surrounded by a distinct bundle sheath; large vessels 1 or 2 present in each larger fibrovascular bundle, absent in smaller fibrovascular bundle; phloem strands 2, V-shaped, in larger fibrovascular bundles separated beneath xylem by parenchyma; in smaller fibrovascular bundles united beneath xylem; fibers extending as girders, adaxially to aquiferous parenchyma and abaxially to hypodermis; bundles of subepidermal sclerified cells 1(2) cell-layers thick present beneath adaxial surface. Figure 4G.

Pedicel anatomy. Triangular in transverse section; fibrovascular bundles 6; belt of sclerified cells present.

Distribution. *Vellozia religiosa* is endemic to three localities in Barra da Estiva and Piatã, in the southern part of Espinhaço chain in Bahia. It occurs in Piatã, near the city and also at Serra do Gentio in the locality of Três Morros, and between Barra da Estiva and Jussiape, along the old road to Mucugê. It was observed to grow in small populations on rocky outcrops, at elevations from 1200 to 1400 m. Figure 5B.

Phenology. *Vellozia religiosa* has been collected with flowers in March and with fruits in February to April.

IUCN Red List category. There are only three currently known relatively small populations of *Vellozia religiosa*. Nevertheless, they occur over non-utilizable grounds, so its conservation status is probably best described as Least Concern (LC), according to IUCN (2001) criteria.

Etymology. The epithet of the new species is coined after the population that grows along the pilgrimage track to Senhor do Bonfim (Our Lord of the Good End) chapel, on the slopes of Serra de Sant'Ana (St. Anne Mountains), near Piatã.

Discussion. In cladistics analyses *Vellozia religiosa* has been sister to *V. jolyi* (Mello-Silva et al., 2011) but differs by having minor fibrovascular bundles in the leaves, which are themselves more erect, narrower, mucronate, and pungent. The individuals tend also to be less robust than individuals from *V. jolyi*, although the flowers, having 12 stamens, are quite similar to those from southern populations of *V. jolyi*. Both species are, in addition, allopatric.

Paratypes. BRAZIL. **Bahia:** Barra de Estiva, Serra do Sincorá, ca. 15–19 km W of Barra da Estiva, on rd. to Jussiape, 13°35'S 41°27'W, *R. M. Harley* 20737 (CEPEC not seen, K not seen, SPF [2]); Piatã, Serra de Santana, 13°09'S 41°46'W, *L. P. Queiroz* H51524 (CEPEC not seen, HUEFS not seen, K, SPF); Serra de Santana, track to Senhor do Bonfim chapel, immediately E of town, 13°09'04"S 41°45'54"W, *R. Mello-Silva* 2577 (SPF).

KEY TO VELLOZIA HEMISPHERICA GROUP SPECIES AMONG BRAZILIAN VELLOZIACEAE

- 1a. Corona always present, with flattened (petaloid) appendages; stamens 6; stigma capitate, clavate, linear or subapical *Barbacenia* Vand.
- 1b. Corona absent or with fringed or alate appendages; stamens (6 to)18–36(to 74); stigma trilobate-peltate ... *Vellozia* Vand.

- 2a. Ovary and fruit as long as or, generally, longer than broad *Vellozia*, excluding *V. hemisphaerica* group
- 2b. Ovary and fruit broader than long *Vellozia hemisphaerica* group
 - 3a. Leaf without abscission line, leaf blade persistent and reflexed 3. *V. hemisphaerica* Seub.
 - 3b. Leaf with abscission line, leaf blade deciduous.
 - 4a. Leaf apex abruptly acute; phyllotaxis spirotristichous.
 - 5a. Dry leaf blade revolute, apex not mucronate; stamens 12 to 18; minor fibrovascular bundles in leaf absent 4. *V. jolyi* L. B. Sm.
 - 5b. Dry leaf blade involute, apex mucronate; stamens 12; minor fibrovascular bundles in leaf present 5. *V. religiosa* Mello-Silva & D. Sasaki
 - 4b. Leaf apex long attenuate to caudate; phyllotaxis tristichous.
 - 6a. Stem 80–300 cm; stamens 48 to 66; corona present; flowers 1 to 3, subsidiary cells ridged 1. *V. canelinha* Mello-Silva
 - 6b. Stem 3.5–35 cm; stamens (16 to)18; corona absent; flower 1, subsidiary cells smooth 2. *V. caudata* Mello-Silva

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TAXONOMIC REVISION OF *ALOYSIA* (VERBENACEAE, LANTANEAE) IN SOUTH AMERICA¹

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ABSTRACT

Aloysia Paláu is the third largest genus of tribe Lantaneae, after *Lippia* L. and *Lantana* L., in the Verbenaceae. Recent molecular phylogenetic studies have circumscribed genus *Aloysia* as 31 species, with the transfer of most species of *Acantholippia* Griseb. and the inclusion of the monotypic *Xeroalloysia* Tronc., as well as the exclusion of several North American *Aloysia* species that nest within a *Lippia*–*Lantana* clade. Newly circumscribed *Aloysia* are found mostly in South America, where the genus is represented by 28 species and six varieties. Only four *Aloysia* species are found in North America, *A. coalcomana* Siedo, *A. macrostachya* (Torr.) Moldenke, *A. wrightii* A. Heller, and *A. gratissima* (Gillies & Hook.) Tronc. var. *gratissima*, this last being the only taxon found in both North and South America. A taxonomic revision of the genus *Aloysia* for South America is provided with detailed morphological descriptions, as well as keys for taxonomic identification, illustrations or indication of iconography, and distribution and herbarium specimen lists. The genus *Xeroalloysia* Tronc. is here considered a synonym of *Aloysia*, and nine new taxonomic synonyms are here established. Lectotypification is designated for *Verbena* L. sect. *Aloysioides* Walp., and neotypification is designated for *V. salviifolia* Hook. & Arn.

Key words: *Acantholippia*, *Aloysia*, South America, Verbenaceae.

Recent molecular phylogenetic studies dealing with generic limits in the Lantaneae (Verbenaceae) have suggested that *Aloysia* Paláu, as traditionally circumscribed, may be a polyphyletic group (Marx et al., 2010; Lu-Irving & Olmstead, 2013). A subsequent study that focused on resolving the position of *Aloysia* and related genera (Lu-Irving et al., 2014), using both chloroplast and nuclear gene sequences, confirmed the non-monophyly of traditional *Aloysia*. These authors proposed the inclusion within *Aloysia* of most taxa in *Acantholippia* Griseb. and the monotypic genus *Xeroalloysia* Tronc., and the exclusion of several North American taxa nested in the *Lantana* L.–*Lippia* L. clade (Lu-Irving et al., 2014: 649, fig. 4), to be able to recover a well-supported monophyletic *Aloysia*. Consequently, this new circumscription of *Aloysia* comprises 31 species, which occur in four major and consistently inferred clades. One clade groups the majority of *Aloysia* taxa; a second clade groups the type species of *Aloysia*, *A.*

citrodora Paláu, plus another species that shares its inflorescence morphology; a third clade reunites two South American *Aloysia* taxa; and a fourth clade groups the type species of *Acantholippia* together with the rest of the taxa formerly in *Acantholippia*. The *Lantana*–*Lippia* clade is a strongly supported group that includes *Phyla* Lour. and *Nashia* Millsp., as well as three Mexican species of *Aloysia* (*A. barbata* (Brandege) Moldenke, *A. chiapensis* Moldenke, and *A. sonorensis* Moldenke), and *Acantholippia seriphioides* (A. Gray) Moldenke.

Aloysia is the third largest genus of tribe Lantaneae, after *Lippia* and *Lantana*. *Aloysia* is distinguished from *Lantana* by its dry fruit, being fleshy in the last, and from *Lippia* by its long racemose florescences with the rachis longer than the peduncle, and alternate or opposite flowers; in *Lippia*, florescences are capituliform with a brief rachis and longer peduncle, and flowers are spiraled. Sanders (2001: 310) states *Aloysia* is based on two synapo-

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morphies, “inconspicuous, ephemeral floral bracts and involute calyx lobes.” Lu-Irving et al. (2014) noted the 4-lobed calyx as the defining feature for newly circumscribed *Aloysia*, as had been suggested by previous studies (O'Leary et al., 2012).

Aloysia as newly circumscribed is almost exclusively found in South America, with only three species restricted to North America. *Aloysia wrightii* (A. Gray) A. Heller and *A. macrostachya* (Torr.) Moldenke occur in the southwestern United States, extending into Baja California and across northern Mexico; *A. coalcomana* is only known from one locality in Michocán, Mexico. These three species are not further considered here. Lu-Irving et al. (2014) stated that shifts in geographic range from subtropical South America to North America must have occurred at least twice in *Aloysia*, based on the reconstruction of the geographical distribution of species in the phylogenetic trees (2014: 651, fig. 5). However, based on these results, Lu-Irving et al. (2014) could not ascertain if the three North American *Aloysia* taxa were the result of long-distance dispersal or northward migration via the Andes.

Lu-Irving and Olmstead (2011; 2013) and Lu-Irving et al. (2014) found South American *Aloysia* comprised of several small lineages and one larger lineage containing the majority of *Aloysia* species. This large clade includes the formerly monotypic genus *Xeroaloyisia* as well as the North American *Aloysia* taxa; all exemplars have homothetic pleiobotrya (only axillary florescences). This species assemblage seems to represent a recent radiation, because branch lengths were short throughout the clade (Lu-Irving et al., 2014). *Aloysia* species with heterothetic pleiobotrya (both axillary and terminal florescences) grouped together in another clade, in basal position relative to the larger *Aloysia* clade. Taxa formerly in *Acantholippia* with monobotrya (only terminal florescences) also formed a clade, basal to the rest of *Aloysia*. Consequently, inflorescence morphology seems to have phylogenetic significance in *Aloysia*.

There has been no comprehensive taxonomic revision of *Aloysia*. A Ph.D. dissertation, which unfortunately lacks illustrations (Siedo, 2006), considered 30 species and 14 varieties, seven species from North America and the remaining 23 species from South America. This work included a phylogenetic analysis based on 50 morphological characters, and the results supported the monophyly of *Aloysia*. However, the author mentioned that preliminary molecular phylogenetic analysis conducted by the Olmstead et al. laboratory suggested the contrary, resulting in a polyphyletic *Aloysia*, and that additional studies were needed. This further investigation

was performed by Lu-Irving et al. (2014), with the taxonomic implications being followed in this present work.

Partial treatments have been done for *Aloysia* in Argentina (Troncoso, 1962, 1974; Botta, 1979, 1993; Múlgura et al., 2012), recognizing ca. 10 species. In Bolivia, Wood (2009) recognized seven species, and in Venezuela, López Palacios (1977) mentioned one species. However, no overall revision of the entire genus has ever been published. Four new species of *Aloysia* were recently described by Siedo (2012) for Brazil, Peru, and Mexico.

Revision of *Aloysia* for South America is presented here, following new taxonomic circumscription as suggested by the phylogenetic evidence of Lu-Irving et al. (2014). Illustration or reference to iconography, citation of representative material, synonymy, and any pertinent typification are included for the 28 species and six varieties in South America as considered herein.

MATERIALS AND METHODS

This taxonomic revision is based on collections from the following herbaria: BAF, CONC, F, K, LIL, MO, NY, P, SGO, SI, ULS, US, and WTU. Flower measurements were taken from material rehydrated by boiling. Fruit measurements were taken from dried specimens. The descriptive terminology of the inflorescences used here is in accordance with Múlgura et al. (2002), the morphological terms follow Hickey (1974), and the description of pubescence corresponds to that of Lawrence (1951). Inflorescence morphology follows terminology used by Múlgura et al. (2002), which follows Troll (1964–1969) and Sell (1976, 1980). Distribution and habitat data for taxa were taken from the herbarium specimen labels. A list of accepted species and varieties of *Aloysia* (Appendix 1), an index to collectors (Appendix 2), and a list of taxa newly synonymized here with their accepted range (Appendix 3) are provided.

TAXONOMIC TREATMENT

***Aloysia* Paláu, Parte Práct. Bot. 1: 767. 1784. TYPE:**
Aloysia citrodora Paláu.

Aloysia Ort. ex Juss., Ann. Mus. Hist. Nat. 7: 73. 1806, nom. illeg. *Lippia* L. sect. *Aloysia* (Ort.) Schauer in DC., Prod. [de Candolle] 11: 572. 1847, nom. illeg. *Lippia* subg. *Aloysia* (Ort.) Schauer in Engl. & Prantl, Nat. Pflanzenfam. Teil 4(Abt. 3a): 151. 1897, nom. illeg. TYPE: *Verbena triphylla* L'Hér. [= *A. triphylla* (L'Hér.) Britton; = *A. citrodora* Paláu].

Verbena L. sect. *Aloysioides* Walp., Repert. Bot. Syst. 4: 13. 1845. TYPE: *Verbena gratissima* Gillies & Hook. [= *Aloysia gratissima* (Gillies & Hook.) Tronc.], lectotype, designated here.

Zapania Lam., Tabl. Encycl. 1: 59. 1791, nom. illeg. orth.,
Zappania Scop., 1786.

Xeroaloysia Tronc., Darwiniana 12: 50. 1960. syn. nov.
TYPE: *Xeroaloysia ovatifolia* (Moldenke) Troncoso [= *Aloysia ovatifolia* Moldenke, Lilloa 5: 379. 1940].

Plants suffruticose or shrubby, mostly aromatic; stems 4-angled when young, rounded with age, branches sometimes spiny, pubescent or glabrate. Leaves simple, mostly opposite or ternate, 3(4)-whorled, occasionally alternate or clustered into fascicles of 4 to 8 leaves; blades entire or 3- to 5-lobed, exceptionally 3-parted, linear, elliptic, oblong, obovate, ovate, orbicular, rhomboidal, or cordate, sessile, subsessile, or briefly petiolate, basally attenuate, acute, round, truncate, or cordate, apically obtuse, subobtuse, acute, acuminate, or round; blade margins entire, crenate, serrate, dentate, or lobed, sometimes revolute or subrevolute; adaxially glabrous or scabrous, hispidulous, or strigose; abaxially strigose, incanous, hirsute or hispid, often with glandular trichomes, membranaceous, coriaceous, or somewhat thickened texture. Inflorescences in spicate racemes, occasionally paniculate; florescences globose, or filiform in anthesis, elongated or not in fructification, sessile or subsessile, in monobotrya or grouped as pleiobotrya in terminal and axillary (heterothetic) or only axillary (homothetic) positions; flowers often in clusters of 3 to 6; sessile to briefly pedicellate, subtended by floral bracts; bracts inferior to flowers, linear, elliptic, obovate, or ovate; abaxially strigose to setose; apically acute to acuminate. Flower with the calyx 4-toothed, exceptionally bilobed, subactinomorphic to zygomorphic, externally strigose, setose, hirsute, or velutinous, often subsessile glandular, internally glabrous; fully accrescent in fruit and persistently enclosing mature schizocarp; corollas subactinomorphic to zygomorphic, infundibuliform, white, lavender, purple, pink, or blue; tube cylindrical to gibbous, glabrous to variously pubescent externally, internally villous along distal half; limb 4-lobed, superior lobe often cleft; styles filiform and usually glabrous, occasionally villous along base; stigmas capitate to subcapitate, bilobed, stigmatic lobes approximately equal or oblique, apically or laterally disposed; stamens 4, epipetalous, subequal to didynamous, the superior pair sometimes weakly exerted, exceptionally with glandular anther connective appendices; thecae longitudinally dehiscent. Fruit a dry schizocarp, exceptionally drupaceous; the dry schizocarp composed of 2 cluses (each cluse is a unit representing half a carpel, derived from a unicarpellate ovary splitting into 2), ellipsoid to obovoid, often \pm cordate, basally truncate, apically rounded to bilobed, glabrous or setose pubescence, typically elliptic in cross section and commissural

faces not connate, exceptionally orbicular in cross section, commissural faces connate.

Distribution. *Aloysia* is an American genus, occurring from southwestern United States and Mexico to Chile and central Argentina. It is most diverse in South America, with 28 species and six varieties occurring there (Appendix 1). One taxon, *A. gratissima* var. *gratissima* (Gillies & Hook.) Tronc., is found in both North America (Texas, Arizona) and South America, with a disjunction in distribution across the tropics. Only three *Aloysia* species are found exclusively in North America, *A. coalcomana* Siedo, *A. macrostachya* (Torr.) Moldenke, and *A. wrightii* A. Heller, and are not further considered here.

Notes. Walpers (1845) established *Verbena* sect. *Aloysioides*, mentioning the two species *V. salviifolia* Hook. & Arn. and *V. gratissima* Gillies & Hook. The latter name is selected as lectotype (McNeill et al., 2012, Art. 10.2) because it is a species that certainly belongs within *Aloysia* and is representative of the genus.

The fruit in *Aloysia* is a schizocarp that derives from a unicarpellate ovary that normally (except in *A. ovatifolia* Moldenke, which has an undivided drupaceous fruit) separates into two units along the medial plane of the ovary; each unit represents half a carpel and is called a cluse (O'Leary et al., 2012).

The term florescence is used to define a minimum expression of flower arrangement. In the Verbenaceae, florescences are either racemes or spikes that vary in the arrangement, spacing, number of flowers, and development of its rachis. Florescences are organized into simple inflorescences, as monobotrya, or compound inflorescences, as pleiobotrya. In pleiobotrya, florescences may be either terminal or axillary, as heterothetic pleiobotrya, or grouped only as axillary florescences, as homothetic pleiobotrya (Múlgura et al., 2002; O'Leary et al., 2012). Classical views of inflorescence evolution (Troll, 1964–1969; Sell, 1976; 1980) suggest that heterothetic pleiobotrya gave rise, on the one hand, to homothetic pleiobotrya by loss of the terminal florescence, and, on the other hand, to monobotrya, by loss of axillary florescences (O'Leary et al., 2012). Homothetic pleiobotrya and monobotrya can therefore be considered derived conditions. This analysis also confirms the derivation of monobotrya from heterothetic pleiobotrya by loss of axillary florescences. However, unexpectedly, according to classical assumptions about the evolution of inflorescences, reversions from monobotrya to heterothetic pleiobotrya also occur.

Within *Aloysia*, the most frequent inflorescence morphology in South America is a homothetic

pleiobotrya, found in 19 out of the 28 taxa. There are only five species with heterothetic pleiobotrya: *A. arequipensis* Siedo (cf. Fig. 1), *A. citrodora*, *A. fiebrigii* (Hayek) Moldenke, *A. herrerae* Moldenke (Fig. 7), and *A. velutina* Siedo (Fig. 13). Monobotrya are found in four out of the five *Acantholippia* species recently transferred to *Aloysia* (Lu-Irving et al., 2014): *A. deserticola* (Phil.) Lu-Irving & N. O’Leary, *A. riojana* (Hieron. ex Moldenke) Lu-Irving & N. O’Leary, *A. salsoloides* (Griseb.) Lu-Irving & N. O’Leary, and *A. tarapacana* (Botta) Lu-Irving & N. O’Leary.

The base chromosome number in *Aloysia* seems to be $x = 9$, based on a specimen of *A. gratissima*, although this is the lowest observed count in the genus (Powell et al., 2010). This is in agreement with other Lantaneae, and both *Lippia* and *Phyla* would also appear to have $x = 9$ (Sanders, 1987; Munir, 1993). In contrast, *Lantana* is reported to have a base chromosome number of $x = 11$ or 12 (Sanders, 1987).

TAXONOMIC KEY TO SPECIES OF *ALOYSIA* FROM SOUTH AMERICA

- 1. Plants with spiny branches and reduced leaf blades, always shorter than 0.5 cm long 2
- 1'. Plants with no spiny branches and developed leaf blades, always longer than 0.5 cm long 5
- 2(1). Leaves alternate, not squamiform, nor imbricate, blades 5-lobed 22. *A. salsoloides* (Griseb.) Lu-Irving & N. O’Leary
- 2'. Leaves opposite, squamiform, densely imbricate, blades entire or 3-lobed 3
- 3(2'). Leaf blades entire and no evident furrows on abaxial surface, dark green colored, endemic to Chile 25. *A. tarapacana* (Botta) Lu-Irving & N. O’Leary
- 3'. Leaf blades 3-lobed, with a conspicuous furrow on each blade lobe, light green or yellow-green colored, Argentina and Chile 4
- 4(3'). Fruits typical of the genus with cluses (each cluse is a unit representing half a carpel, derived from a unicarpellate ovary splitting into two) of elliptic cross section and commissural faces not connate 9. *A. deserticola* (Phil.) Lu-Irving & N. O’Leary
- 4'. Fruits with cluses of orbicular cross section and connate commissural faces ... 21. *A. riojana* (Hieron. ex Moldenke) Lu-Irving & N. O’Leary
- 5(1'). Fruits undivided and drupaceous 16. *A. ovatifolia* Moldenke
- 5'. Fruits schizocarpic and divided into two dry cluses 6
- 6(5'). Leaves alternate 19. *A. polystachya* (Griseb.) Moldenke
- 6'. Leaves opposite or verticillate (ternate) 7
- 7(6'). Leaves mostly verticillate (ternate), sometimes opposite at some nodes 8
- 7'. Leaves mostly opposite, sometimes verticillate at some nodes 13
- 8(7). Florescences only axillary 9
- 8'. Florescences axillary and terminal 12

- 9(8). Leaves evenly crenate toward apex 8. *A. crenata* Moldenke
- 9'. Leaves with entire margins 10
- 10(9'). Leaves adpressed to the stem, sessile, with ovate, elliptic, or cordate blades 11
- 10'. Leaves not adpressed to the stem, with sessile to subpetiolate, elliptic blades 2. *A. brasiliensis* Moldenke
- 11(10). Leaf blades ovate to elliptic 18. *A. polygalifolia* Cham.
- 11'. Leaf blades cordate 7. *A. cordata* Siedo
- 12(8'). Leaf blades smaller, $1.8\text{--}3 \times 0.2\text{--}0.5$ cm, with entire margins 11. *A. fiebrigii* (Hayek) Moldenke
- 12'. Leaf blades larger, $2\text{--}8 \times 1\text{--}2.5$ cm, with entire or slightly serrate margins 6. *A. citrodora* Paláu
- 13(7'). Florescences terminal and axillary; plants endemic to Peru and Bolivia 14
- 13'. Florescences only axillary 16
- 14(13). Leaf margins entire, with minute scabrous pubescence on abaxial blade surface, glabrous adaxially 14. *A. herrerae* Moldenke
- 14'. Leaf margins not entire, with velutinous, incanous, strigose, or tomentose pubescence, never glabrous 15
- 15(14'). Margins slightly crenate along entire blade, adaxially velutinous, abaxially incanous ... 27. *A. velutina* Siedo
- 15'. Margins finely serrate along apical 2/3 to 1/2 of blade length, adaxially strigose, abaxially tomentose 1. *A. arequipensis* Siedo
- 16(13'). Flowers with a bilobulated calyx 10. *A. dusenii* Moldenke
- 16'. Flowers with a 4-toothed calyx 17
- 17(16'). Superior pair of stamens with anther connective appendices glandular 26. *A. trifida* (Gay) Lu-Irving & N. O’Leary
- 17'. Superior pair of stamens with anther connective appendices not glandular 18
- 18(17'). Leaf margins completely entire, sometimes slightly serrate toward apex 19
- 18'. Leaf margins not entire, ranging from serrate or crenate to dentate, or basally entire with some serration, crenation, or dentition in some portion of the blade; if margins entire, then only on leaves on some part of the plant, the remaining leaves not entire 22
- 19(18). Leaves smaller, narrowly elliptic, less than 2×0.3 cm 12. *A. gratissima* (Gillies & Hook.) Tronc.
- 19'. Leaves larger, elliptic, ovate, cordate, or obovate, more than 2×0.3 cm 20
- 20(19'). Leaf adaxial surfaces without a conspicuous midvein, leaves briefly petiolate, with blades elliptic, obovate, or ovate 21
- 20'. Leaf adaxial surfaces with conspicuous midvein, leaves sessile, with blades obovate to oblanceolate 15. *A. oblanceolata* Moldenke
- 21(20). Leaf blades elliptic to obovate, with obtuse apex 20. *A. pulchra* (Briq.) Moldenke
- 21'. Leaf blades elliptic to ovate, with acute to subobtuse apex 12. *A. gratissima* (Gillies & Hook. ex Hook.) Tronc.
- 22(18'). Leaf margins almost entirely dentate, crenate, or serrate 23

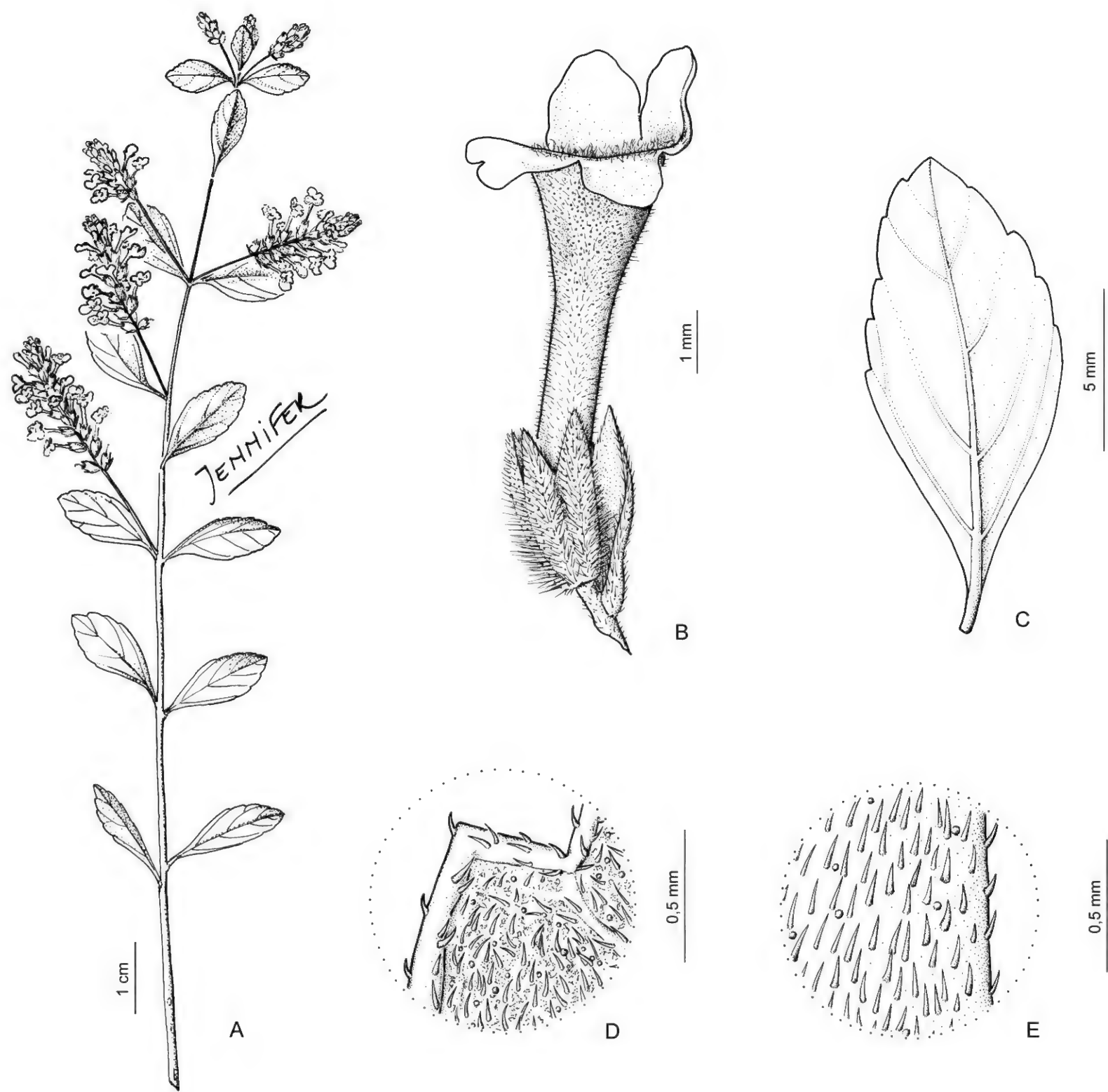


Figure 1. *Aloysia arequipensis* Siedo. —A. Floriferous branch with florescences in both axillary and terminal positions (heterothetic pleiobotrya). —B. Lateral view of intact flower with calyx and floral bract. —C. Intact leaf, adaxial surface. —D. Detail of tomentose pubescence on abaxial blade surface. —E. Detail of strigose pubescence on adaxial blade surface. A–E, illustrated from Pennell 13079 (type, US).

22'.	Leaf margins with some serration or denticulation in some portion of the blade, but always entire basally	31	1 or 2(3) per leaf axil or grouped toward plant apex	4. <i>A. catamarcensis</i> Moldenke
23(22).	Leaf margins with 3 to 5 deep teeth coarsely dentate or serrate on each side	26	25'.	Florescences dense or lax, cylindrical, 1–12 cm long, 1 per leaf axil
 5. <i>A. chamaedryfolia</i> Cham.	26(25').		Leaf blades oblong, 1–4.5 × 0.15–1 cm ..
23'.	Leaf margins evenly dentate, crenate, or serrate	24	 3. <i>A. castellanosi</i> Moldenke
24(23').	Leaf margins minutely serrate or crenate; corolla less than 4 mm long; calyx with long teeth, equaling or exceeding calyx tube in length	25	26'.	Leaf blades elliptic, ovate, or orbicular, 1–5(–7) × 1–3(–4) cm
24'.	Leaf margins notoriously crenate or dentate; corollas more than 4 mm long; calyx teeth never exceeding calyx tube in length	27	27(25').	Leaves membranaceous and plane; corolla tube more than 6 mm long
25(24').	Florescences dense, subrhomboidal in anthesis, cylindrical in fructification, 2–4 cm long,	27'.	 17. <i>A. peruviana</i> (Turcz.) Moldenke
				Leaves rugose and creased; corolla tube less than 6 mm long; if leaves membranaceous then corolla tube less than 4.5 mm long ..
			 24. <i>A. scorodonioides</i> (Kunth) Cham.

- 28(22). Floral bracts 4–4.5 mm long, surpassing calyx, endemic to Chile
..... 23. *A. salviifolia* (Hook. & Arn.) Moldenke
28'. Floral bracts 1–2 mm long, not surpassing calyx 29
29(28'). Leaf blades elliptic, with slightly serrate margins in apical half, venation conspicuous, reddish brown, pinnate, impressed on abaxial surface, endemic to Brazil (Paraná) 13. *A. hatschbachii* Moldenke
29'. Leaf blades elliptic or ovate, with entire or serrate margins, midvein impressed only on abaxial surface, or if venation pinnate and conspicuous then not reddish brown
..... 12. *A. gratissima* (Gillies & Hook.) Tronc.

1. *Aloysia arequipensis* Siedo, Lundellia 15: 38, fig. 1. 2012. TYPE: Peru. Arequipa: Mpio. Arequipa, Tiabaya, open, rocky slope, 8 Apr. 1925, *F. W. Pennell* 13079 (holotype, NY [barcode] NY01911741 not seen, NY image!; isotypes, F [bc] F0093716F not seen, F image!, GH [bc] GH00359317 not seen, GH image!, US!). Figure 1.

Shrubs 0.5–1.5 m tall; stems glabrous. Leaves opposite, rarely ternate; petioles brief, 1–2 mm; blades elliptic, 1–2 × 0.5–1.2 cm, apex acute to obtuse, base acute, margins finely serrate along apical 2/3 to 1/2 of blade length, adaxially strigose, abaxially tomentose, with an understory of subsessile, glandular trichomes. Florescences terminal and axillary (heterothetic pleiobotrya), cylindrical, loosely spicate, 1–5 cm; peduncles 0.5–2.8 cm; flowers lavender to pink, often with a whitish limb, floral bracts elliptic, 1–3 × 0.5–1 mm, apex acuminate, with strigose pubescence and an understory of subsessile, glandular trichomes. Flower with the calyx 2–4 mm, densely hirsute, with an understory of subsessile, glandular trichomes with 4 brief teeth, unequal, triangular; corolla tube 4–7 mm, externally finely pulverulent, with villous fauce. Cluse 1–1.5 × 1 mm, glabrous.

Distribution and habitat. *Aloysia arequipensis* is endemic to Peru, in arid sites from Arequipa and southern Lima Provinces, at elevations of 2000–3000 m.

Discussion. *Aloysia arequipensis* is one of the five South American taxa distinguished by its heterothetic pleiobotrya, also present in *A. citrodora*, *A. fiebrigii*, *A. herrerae*, and *A. velutina*. However, *A. arequipensis* may be differentiated from *A. citrodora* and *A. fiebrigii* by its opposite leaves, being ternate in these last two species. It is distinguished from *A. herrerae* by its finely serrate leaf blade margins, with blade margins entire in this last taxon. *Aloysia arequipensis*

may be differentiated from *A. velutina* because in this last species leaf blade margins are crenate. *Aloysia arequipensis* is also morphologically similar to *A. scorodonoides* (Kunth) Moldenke var. *hypoleuca* (Briq.) Moldenke from which it is readily distinguished by inflorescence morphology, having only axillary florescences present (homothetic pleiobotrya) in this last taxon.

Selected specimens examined. PERU. **Arequipa:** Arequipa, cerros de Jesús, Vargas 12671 (US). **Lima:** Mpio. Yauyos, Aiza, entre Catahuas y Tupe, Pradera, *E. Cerrate* 1282 (MO).

2. *Aloysia brasiliensis* Moldenke, Phytologia 3: 162. 1949. TYPE: Brazil. Paraná, 4 Jan. 1904, *P. K. Dusén* s.n. (holotype, R [barcode] R000046798 not seen, R image!; isotypes, NY [bc] NY00103867 not seen, NY image!, SI [bc] SI003386!). Figure 2.

Shrubs 1–3 m tall, stems glabrous. Leaves ternate, not adpressed to the stem, sclerophyllous, sessile to subpetiolate, petiole 0.2–1.5 mm, blades narrowly elliptic to elliptic, 1–4(–5) × 0.5–1.5 cm, apex acute or sometimes subobtuse, base acute, margins entire, sometimes subrevolute, scabrous to strigose pubescence on both surfaces. Florescences axillary, solitary, lax, 4–10(–16) cm; peduncles 1–5 cm; flowers lilac; pedicels 0.5–1 mm; floral bracts linear, 2–3.5 mm, apex acuminate, with strigose pubescence. Flower with the calyx 2–4 mm, hispid, 4-toothed, the teeth unequal, triangular; corolla tube 4–5.5 mm, externally finely pulverulent, internally, with villous fauce. Cluse 1.5 × 1 mm, glabrous.

Distribution and habitat. *Aloysia brasiliensis* is endemic to southern Brazil, from the states of Rio Grande do Sul, Paraná, and Santa Catarina. The species has been collected from disturbed habitats, at elevations from 700 to 900 m.

Discussion. *Aloysia brasiliensis*, *A. cordata*, and *A. polygalifolia* all have glabrous stems but puberulent rachises, and sclerophyllous leaves with entire margins, and all three are endemic to Brazil. *Aloysia brasiliensis* differs because leaves are not adpressed to the stem, with elliptic blades, versus leaves adpressed to the stem, with ovate, elliptic, or cordate blades in the other two species. In addition, *A. brasiliensis* has larger leaves (1–4[–5] × 0.5–1.5 cm) with an acute base, versus smaller and a different basal shape in the other two species. Leaf blades in *A. polygalifolia* (0.5–2 × 0.3–1 cm) have a truncate base; blades in *A. cordata* (0.3–1 × 0.3–0.9 cm) have a cordate base.

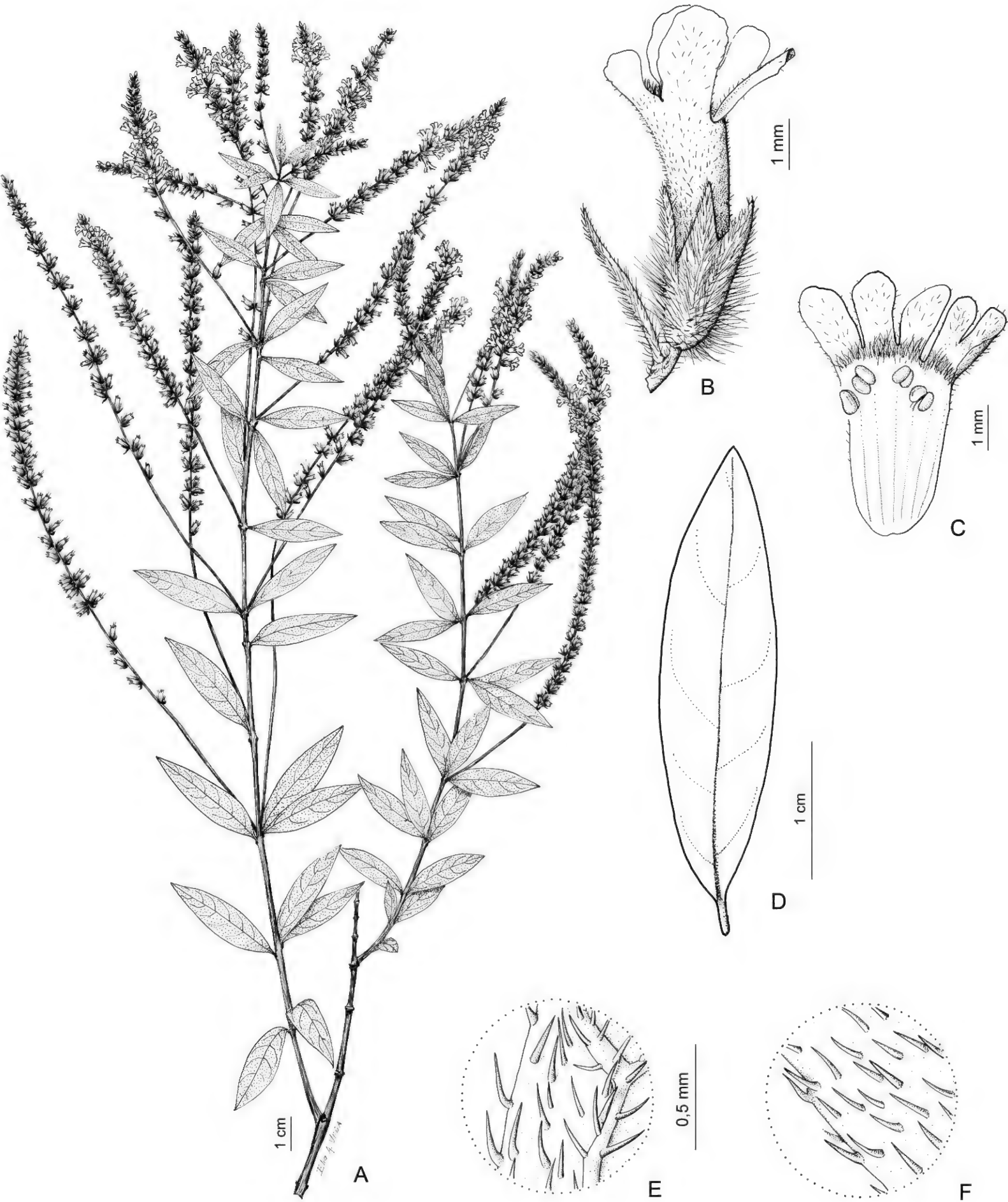


Figure 2. *Aloysia brasiliensis* Moldenke. —A. Floriferous branch, showing the axillary florescences (homothetic pleiobotrya). —B. Intact flower in lateral view, with floral bract subtending the hispid calyx. —C. Corolla dissected open to reveal the androecium. —D. Intact leaf, adaxial surface. —E. Detail of strigose pubescence on blade adaxial surface. —F. Detail of strigose pubescence on abaxial blade surface. A, taken from *Klein 3489* (SI); B–F, from *Hatschbach 14905* (SI).

Selected specimens examined. BRAZIL. **Paraná:** Uniao da Vitoria, Sao Domingos, *Silva 7037* (SI); Uniao da Vitoria, *Hatschbach 14905* (SI). **Rio Grande do Sul:** Nonoai, ad fl. Uruguay, *Rambo 28141* (NY). **Santa Catarina:** Irani, *Smith & Klein 13029* (NY); Caçador, faz. dos Carneiros, *Klein 3489* (SI), *Smith & Reitz 9012* (SI).

3. *Aloysia castellanosi* Moldenke, Lilloa 5: 372. 1940. TYPE: Argentina. San Juan: Quebrada del Zonda, 28 Feb. 1926, *A. Castellanos s.n.* (holotype, BA-26/602!; isotypes, CORD [barcode] CORD00003815 not seen, CORD image!,

NY [bc] NY00103870 not seen, NY image!, SI [bc] SI003376!).

Aloysia castellanosi var. *magna* Moldenke, Known Geogr. Distrib. Verb. Avicenn., 76. 1942. TYPE: Argentina. Tucumán: Valle de Amaicha, Zurita, 4 Feb. 1917, *L. Castillón* 85 (holotype, NY [barcode] NY00103871 not seen, NY image!; isotypes, LIL [bc] LIL001434 not seen, LIL image!, LP [bc] LP006684 not seen, LP image!, SI [bc] SI003387!).

Aloysia decorticans Ravenna, Onira 11(2): 3(–4). 2007. TYPE: Argentina. Salta: Quebrada de Guachipas, 23 Jan. 1943, *Castellanos s.n.* (holotype, BA-46961!).

Plants suffruticose, 1 m tall; stems cylindrical, pilose to subglabrous, internodes 1–4.5 cm, smooth, red, with fallen bark. Leaves opposite; petioles brief, 0.8–4 mm; blades oblong, 1–4.5 × 0.15–1 cm, apex obtuse, base truncate, margins prominently and evenly crenate, blade margins subrevolute, adaxially scabrous, creased, abaxially densely hispid. Florescences axillary, solitary, dense, cylindrical, 1–6 cm in fructification; peduncles 0.5–2.8 cm; flowers white, pink, or violet; floral bracts ovate, obovate, or elliptic, 2.5–10.5 × 1.5–6 mm, sticky glandular on both bract surfaces. Flower with the calyx 2.5–5 mm, densely hirsute, with 4 brief teeth, unequal, triangular; corolla tube 4–7 mm, externally glabrous, with villous fauce. Cluse 2 × 0.5 mm, glabrous.

Iconography. Botta (1979: 73, fig. 1).

Distribution and habitat. *Aloysia castellanosi* is endemic to Argentina, known only from the provinces of Catamarca, La Rioja, Salta, San Juan, and Tucumán. The species is found in the phytogeographic provinces of monte and chaqueña (Cabrera & Willink, 1973), growing at elevations of 2500–2800 m.

Discussion. *Aloysia castellanosi* is distinguished by its leaf morphology, with oblong blades and margins prominently and evenly crenate, and creased texture. This feature makes it hard to confuse with any other species of the genus.

Selected specimens examined. ARGENTINA. **Catamarca:** Andalgalá: 16 km SE from Andalgalá, *Cantino* 693 (SI). **La Rioja:** General Lavalle, Parque Nac. Talampaya, *Botta* 695 (SI). **Salta:** San Carlos, ruta 40 de Cafayate a Cachi, sierra de Quilmes, *Cialdella* 218 (SI). **San Juan:** Caucete, Marayes, *Haene* 93 (SI). **Tucumán:** Tafí, Amaicha del Valle, *Burkart* 22066 (SI).

4. *Aloysia catamarcensis* Moldenke, Known Geogr. Distrib. Verb. Avicenn. 76. 1942. TYPE: Argentina. Catamarca: Quebrada del Tala, 15 Mar. 1909, *L. Castillón* 956 (holotype, NY [barcode] NY00103872 not seen, NY image!;

isotypes, CORD [bc] CORD00003817 not seen, CORD image!, GH [bc] GH00299000 not seen, GH image!, LIL [bc] LIL001435 not seen, LIL image!, LIL [bc] LIL001436 not seen, LIL image!, SI [bc] SI003377!).

Plants suffruticose, 1–1.5 m tall, stems cylindrical, pilose to glabrous, with fallen bark, internodes 3–7 cm. Leaves opposite, sometimes ternate; petioles 0.3–1.5 mm; blades elliptic, 1.5–5 × 1–3 cm, apex acute to subobtusate, base acute, margins prominently and evenly crenate to dentate, scabrous, adaxially rugose, abaxially hispid. Florescences axillary, 1 or 2(3) per leaf axil, grouped toward stem apex, dense, subrhomboidal at anthesis, cylindrical in fructification, 2–4 cm, pedunculate; flowers white, pink, or violet; floral bracts elliptic to obovate, apex attenuate, acuminate, 2.5–3.5 × 1–1.5 mm, surpassing calyx, puberulous. Flower with the calyx short, 1–2 mm, hispid, with 4 brief teeth, unequal, triangular; corolla tube 4–7.5 mm, with glabrous fauce. Cluse 1 × 0.5 mm, glabrous.

Iconography. Botta (1979: 79, fig. 3).

Distribution and habitat. *Aloysia catamarcensis* is endemic to northwestern Argentina, being found in the provinces of Santiago del Estero, La Rioja, Catamarca, and Salta. The species has been observed to grow on slopes of small hills or rises.

Discussion. *Aloysia catamarcensis* is distinguished by its elliptic leaf blades with margins prominently and evenly crenate to dentate. It can be confused with *A. scorodonioides* var. *scorodonioides* or *A. peruviana*. However, these two last taxa have florescences cylindrical in anthesis, 4.5–10 cm long, one per leaf axil, in contrast to the shorter florescences of *A. catamarcensis*, subrhomboidal in anthesis, cylindrical in fructification, 2–4 cm long, one or two (three) per leaf axil or grouped toward the apex of the plant in *A. catamarcensis*.

Selected specimens examined. ARGENTINA. **Catamarca:** Belén, cerrito de la Cruz, *Ulibarri* 332 (SI); Capital, Quebrada de los Nacimientos, *Ulibarri* 950 (SI). **La Rioja:** Chilecito, Miranda, rt. 40 a 16 km de Chilecito, *Olmstead* 2007-82 (SI). **Salta:** La Viña, Km. 77, camino de Cafayate a Salta, *Correa* 4318 (SI). **Santiago del Estero:** Alberdi, entre Donaden y Campo Gallo, s. coll. 43 (SI).

5. *Aloysia chamaedryfolia* Cham., Linnaea 7: 234. 1832. *Lippia chamaedryfolia* (Cham.) Steud., Nomencl. Bot. [Steudel], ed. 2 1: 62. 1841. TYPE: “Brasilia,” s.d., *F. Sellow s.n.* (lectotype, designated by Siedo [2010: 200], W-0032437!; isoelectotypes, BM-643743 not seen, BM image!;

G [barcode] G00208776 not seen, G image!, W-Rchb. 1889-0290180 not seen, W image!).

Shrubs erect, 0.5–2 m tall; stems tetraginous, densely pubescent with retrorse hairs. Leaves opposite, sometimes ternate, subsessile; blades ovate to suborbicular 0.3–3 × 0.7–2 cm, apex subobtuse, base subtruncate, margin slightly revolute, deeply toothed, with 3 to 5 deep teeth coarsely dentate or serrate on each side, adaxially scabrous, abaxially densely strigose, venation conspicuous. Florescences axillary, solitary, lax, 5–15 cm; peduncles 2–4 cm; flowers lilac or purple; floral bracts ovate, apex subulate, 1.5 mm, hispid. Flower with the calyx 2.5 mm, hispid in inferior half, slightly hispid toward apex, calyx with 4 brief teeth, unequal, triangular; corolla tube 3–4 mm, with villous fauce. Cluse 1 × 0.5 mm, pubescent at apex.

Iconography. Botta (1979: 91, fig. 7).

Distribution and habitat. *Aloysia chamaedryfolia* grows in southern Brazil, Uruguay, and northeastern Argentina where it is found in rocky soils.

Discussion. *Aloysia chamaedryfolia* is distinguished by its leaf blades ovate to suborbicular with margins with three to five deep teeth on each side, which makes this species not easily mistaken for any other member of the genus.

Selected specimens examined. ARGENTINA. **Misiones:** San Javier, Balneario 4 Bocas, 11 km SE de San Javier, *Krapovickas* 28868 (CTES, SI). BRAZIL. **Rio Grande do Sul:** Arroio dos Ratos, *Hagelund* 10590 (SI). URUGUAY. **Artigas:** Arroyo Sepulturas, *Bonifacino et al.* 1953 (SI). **Rivera:** *Herter* 158 (NY). **Tacuarembó:** Valle Edén, *Rosengurt* 4967 (SI).

6. *Aloysia citrodora* Paláu, *Parte Prácte Bot.* 1: 768. 1784, as “citriodora.” *Verbena citriodora* (Paláu) Cav., *Descr. Pl.* (Cavanilles) 68. 1802. *Aloysia citriodora* Ort. ex Pers., *Syn. Pl.* 2(1): 139. 1806, nom. superfl. illeg. [cf. Art. 52.1; cites *Verbena triphylla* L’Hér.]. TYPE: unnumbered illustration in Paláu, *Part. Prácte Bot.* 1: 768. 1784 (lectotype, designated by Armada & Barra [1992: 89], icon s.n. in Paláu [1784: 768]).

Verbena triphylla L’Hér., *Stirp.* Nov. 1: 21. 1785. *Zapania citrodora* Lam., *Tab. Encycl.* 1: 59. 1791, nom. illeg. [Art. 52.1, cites *Verbena triphylla* L’Hér., the epithet that ought to have been used]. *Lippia citrodora* Kunth, *Nov. Gen. Sp.* 2: 269. 1818, as “citriodora,” nom. illeg. [cf. Art. 52.1, comb. based on “*Zapania citrodora*” Lam.]. *Lippia triphylla* (L’Hér.) Kuntze, *Revis. Gen. Pl.* 3(3): 253. 1898. *Aloysia triphylla* (L’Hér.) Britton, *Sci. Surv. Porto Rico & Virgin*

Islands 6: 140. 1925, nom. superfl. illeg., non *Aloysia triphylla* Royle, *Ill. Bot. Himal. Mts.*, 299. 1833. TYPE: France. Ile de France, cultivated plant in Jardin de Plantes, Paris, s.d., *C. L. L’Héritier s.n.* (lectotype, designated by Moldenke & Moldenke [1983: 232], P not seen, P image!).

Aloysia sleumeri Moldenke, *Phytologia* 10: 170. 1964. TYPE: Argentina. Catamarca: Belén, Pozo de Piedra, 25–31 ene. 1952, *H. Sleumer & F. Vervoost* 2370 (holotype, US [barcode] US00118880 not seen, US image!; isotypes, TEX-LL [barcode] LL00374941 not seen, TEX-LL image!, SI [bc] SI003401!).

Aloysia triphylla (L’Hér.) Britton f. *serrulata* Moldenke, *Phytologia* 50: 308–309. 1982. TYPE: [cultivated] U.S.A. Indiana: Floyd Co., New Albany, 3 Oct. 1893, *L. H. Bailey* 160 (holotype, BH not seen).

Shrubs 1–3 m tall, aromatic, stems glabrous at maturity, subpendulous. Leaves ternate, briefly petiolate, petioles 1–5 mm; blades elliptic, 2–8 × 1–2.5 cm, apex acute, base acute, margins entire or slightly serrate, blade adaxially scabrous, abaxially glabrate with subsessile glandular trichomes, midvein and pinnate venation conspicuous. Florescences terminal and axillary (heterothetic pleiobotrya), lax, 1–5 cm, the terminal ones grouped as paniculiform inflorescences; flowers white, small; floral bracts reduced, ovate, 1–1.5 mm, scabrous. Flower with the calyx 2.5–3 mm, puberulous, with 4 brief teeth, unequal, triangular; corolla tube 5–6 mm, externally puberulous, with villous fauce. Cluse 2 × 1 mm, glabrous or pubescent at apex.

Iconography. Botta (1979: 104, fig. 12).

Distribution and habitat. *Aloysia citrodora* is native to the dry areas of northwestern Argentina, including the provinces of Catamarca, Jujuy, La Rioja, Salta, San Juan, and Tucumán, to southern Bolivia and Paraguay. The species is cultivated all around the world.

Discussion. *Aloysia citrodora* has strongly lemon-scented leaves, which easily distinguishes it from other species, and is often cultivated for the preparation of aromatic teas with medicinal properties. For this reason the taxon is widely cultivated in Chile, Uruguay, southern Brazil, and Paraguay (Arambarri et al., 2009: 18). It can be confused with *A. friebrii*, which also has ternate leaves. However, in this last species, blades are smaller, 1.8–3 × 0.2–0.5 cm, and the blade margin is always entire, in contrast to the blades 2–8 × 1–2.5 cm in *A. citrodora*, which are also entire but sometimes with a slightly serrate margin.

Moldenke (1982: 309) noted that the type for *Aloysia triphylla* f. *serrulata* was collected “from the garden of Cornell Experiment Station. . .from material

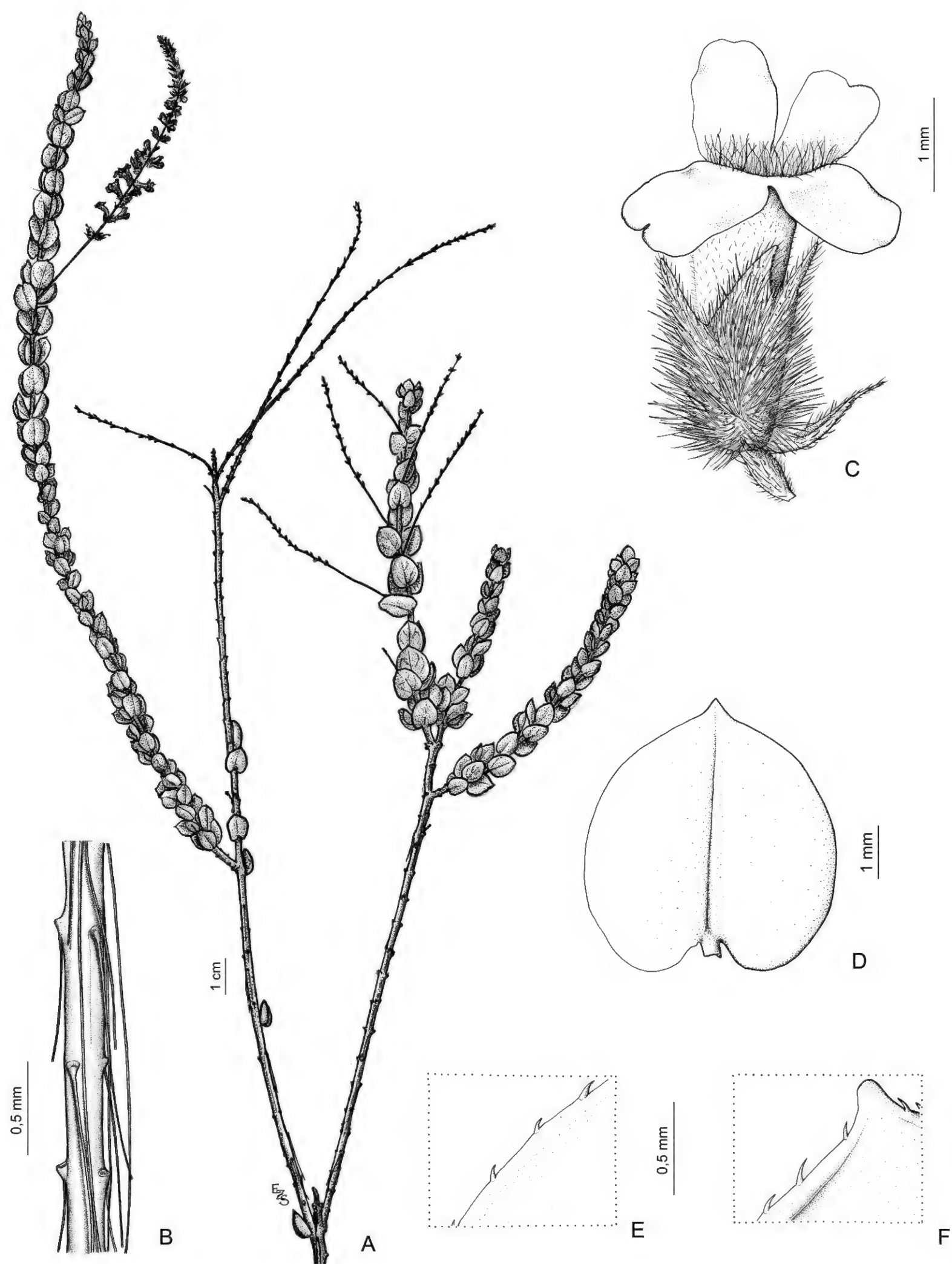


Figure 3. *Aloysia cordata* Siedo. —A. Floriferous branches, showing the axillary florescences (homothetic pleiobotrya). —B. Detail of stem with leaf scars and antrorse pubescence. —C. Lateral view of intact flower, with hispid floral bract. —D. Cordate shape of leaf adaxial surface. —E. Detail of leaf adaxial surface, glabrous with minutely scabrous margins. —F. Detail of leaf abaxial surface, glabrous with minutely scabrous margins. A–F, taken from *Hatschbach 20792* (isotype, SI).

secured from Ernest Walker of New Albany, Indiana.” Even though described from North America, this was a cultivated form of *A. citrodora* native to Argentina.

Cavanilles spelled the epithet *citriodora* with a second “i.” This spelling is correctable (McNeill et al., 2012, Art. 60.8) by omitting the second “i” for *citrodora*.

Selected specimens examined. ARGENTINA. **Catamarca:** Belén, Pozo de Piedra, *Troncoso* 1897 (NY, SI). **Jujuy:** Tumbaya, Chicayo, finca del Sr. Gronda subiendo cerro, *Zuloaga* 10188 (SI); Volcán Chicayo, *Cabrera* 16877 (SI). **La Rioja:** Famatina, La Aguadita, *Cabrera* 24637 (SI). **Salta:** Rosario de Lerma, rt. 51 de Salta a San Antonio de los Cobres, *Olmstead* 2007-13 (SI). **San Juan:** Valle Fértil, de Sa. De Elizondo a Sa. De Chavez, *Kiesling* 6620 (SI). **Tucumán:** Juan Bautista Alberdi, El Chorro, cumbres Calchaquies, *D. Rodríguez* 1214 (NY, SI). BOLIVIA. **Cochabamba:** Carrasco, *E. Martinez* 479 (NY). **La Paz:** Murillo, Calacoto, *Solomon* 15755 (SI). **Tarija:** Mendez, rio Pilaya, Camaron, *Gerold* 161 (SI). PARAGUAY. **Cordillera:** *Schinini* 6767 (NY). **Dpto. Central:** Itá, *Arenas* 1918 (BACP).

7. *Aloysia cordata* Siedo, *Lundellia* 15: 42, fig. 3. 2012. TYPE: Brazil. Paraná: Mpio. São José dos Pinhaes; Río Pequeno, do brejo, 17 Jan. 1969, *G. Hatschbach* 20792 (holotype, NY [barcode] NY01911743 not seen, NY image!; isotypes, K!, MICH!, MO!, SI [bc] SI041007!, SI [bc] SI041008!, UC!). Figure 3.

Shrubs 1–2 m tall, slender, few-branched. Leaves ternate, antrorsely adpressed to the stem, internodes highly regular in length, sessile; blades cordate, sclerophyllous, $0.3\text{--}1 \times 0.3\text{--}0.9$ cm, apex mucronulate, base cordate, margins entire, minutely scaberrulous, adaxially glabrous, smooth, lustrous, abaxially glabrous, smooth, satin-lustrous. Florescences axillary, solitary, lax, 4–12 cm; peduncles 1–3 cm, strigulose; flowers lilac; pedicels 0.5–1 mm; floral bracts linear, 1–1.5 mm, apex acuminate, with strigose pubescence. Flower with the calyx 1.5–2 mm, setose, glandular, 4-toothed, the teeth unequal, triangular; corolla tube 2.5–3.5 mm, externally finely pulverulent, internally, with villous fauce. Cluse 1.5×1 mm, glabrous.

Distribution and habitat. *Aloysia cordata* is endemic to Brazil, from the state of Paraná, where it is found on wet soils.

Discussion. *Aloysia cordata* is similar to *A. polygalifolia* in having leaves adpressed to the stem and sessile, but it is distinguished by its cordate leaf blades (vs. ovate to elliptic in *A. polygalifolia*) and its glabrate leaf surfaces (vs. scabrous to strigose). Both

species occur in Brazil, while *A. cordata* is restricted to eastern Paraná. *Aloysia polygalifolia* is more broadly distributed, from the states of Paraná, Rio Grande do Sul, and Santa Catarina. *Aloysia brasiliensis* also occurs in Paraná, in sympatry with these two species; however, it is easily distinguished by its leaves not adpressed to the stem, with elliptic blades (see discussion under *A. brasiliensis*).

Selected specimens examined. BRAZIL. **Paraná:** San José dos Pinhais, rio Pequeno, *Hatschbach* 20792 (SI); Piraquara, Medianeira, *Costa & Barbosa* 6 (SI).

8. *Aloysia crenata* Moldenke, *Phytologia* 9: 182. 1963. TYPE: Paraguay. Alto Paraná: in regione fluminis, 1909–1910, *K. Fiebrig* 6137 (holotype, US [barcode] US00118876 not seen, US image!; isotypes, BM [bc] BM000098774 not seen, BM image!, GH [bc] GH00282999 not seen, GH image!, LIL [bc] LIL001364 not seen, LIL image!, TEX-LL [bc] LL00374936 not seen, TEX-LL image!, SI [bc] SI003382!, SI [bc] SI003381!, W not seen).

Aloysia krapovickasii Moldenke, *Phytologia* 47: 330. 1981. TYPE: Argentina. Corrientes: Ituzaingó, 24 Sep. 1974, *C. L. Cristobal*, *J. M. Gonzalez*, *A. Schinini*, *C. Quarin*, *M. M. Arbo* & *A. Krapovickas* 26439 (holotype, TEX-LL [barcode] LL00374493 not seen, TEX-LL image!; isotypes, CTES [bc] CTES0013814 not seen, CTES image!, SI [bc] SI003402!).

Shrubs 1–2 m tall; stems cylindrical, densely strigose. Leaves ternate, rarely 2 or 4 per node, subsessile, blades elliptic to obovate, $3.5\text{--}7 \times 1\text{--}2.5$ cm, apex acute to subobtuse, base acute, margin entire toward base, evenly crenate toward apex, conspicuously reticulate venation, adaxially scabrous, abaxially dense strigose with subsessile glandular trichomes underneath. Florescences axillary, solitary, lax, 10–15 cm; peduncles 2–4 cm; flowers white, floral bracts linear, with subulate apex, 2.5–4 mm, hispid. Flower with the calyx 4 mm, hispid in the inferior half, slightly hispid toward apex, with 4 brief teeth, unequal, triangular; corolla tube 7 mm, with villous fauce. Cluse 2×0.5 mm, pubescent in apex.

Iconography. Botta (1979: 100, fig. 10).

Distribution and habitat. *Aloysia crenata* is found from eastern Paraguay to northeastern Argentina (Corrientes) and in Brazil (Paraná).

Discussion. *Aloysia crenata* is distinguished by its ternate leaves with evenly crenate blade margins toward the apex and the presence of only axillary florescences. Other species that have ternate leaves

and only axillary florescences (*A. brasiliensis*, *A. cordata*, and *A. polygalifolia*) can be differentiated by their entire leaf blade margins.

The type specimens of both species *Aloysia crenata* and *A. krapovickasii* are from areas in close proximity to one another, and both specimens are nearly identical morphologically. Thus, *A. krapovickasii* is conspecific and considered a synonym of *A. crenata*, as previously established in Múlgura et al. (2012).

Selected specimens examined. ARGENTINA. **Corrientes:** Ituzaingó, rte. 39 a 10 km de rte. 14, *Cabrera* 29106 (SI). BRAZIL. **Paraná:** *Hatschbach* 26325 (SI). PARAGUAY. **Caazapá:** San Juan Neponuseno, *Rojas* 5903 (SI).

9. *Aloysia deserticola* (Phil.) Lu-Irving & N. O'Leary, Syst. Bot. 39(2): 653. 2014. Basionym: *Lippia deserticola* Phil., *Anales Univ. Chile* 59: 262. 1881, replacement name. Replaced synonym: *Lippia microphylla* Phil., *Anal. Univ. Chile* 27: 350. 1865, non *Lippia microphylla* Cham., *Linnaea* 7: 226. 1832. *Acantholippia deserticola* (Phil.) Moldenke, *Lilloa* 5: 370. 1940. *Acantholippia punensis* (Phil.) Botta, *Hickenia* 1(35): 195. 1979, nom. illeg. superfl. TYPE: Chile. "Frequens in parte boreali deserti Atacama," s.d., *R. A. Philippi s.n.* (lectotype, designated by Múlgura et al. [2012: 5] SGO-4230 not seen, SGO-4230 image!).

Shrubs 0.4–1.5 m tall, with spiny branches; stems hispid, but glabrous at maturity. Leaves small, opposite, adpressed to the stem, sessile, squamiform, imbricate; blades rhomboidal, 1.5×1.5 –2 mm, 3-lobed with a large apical and 1 lateral small lobe on each side, somewhat thicker texture, apex subobtuse, base rounded, margin entire, revolute, adaxially scabrous, abaxially with a conspicuous hirsute furrow on each blade lobe, light green or yellow-green in color. Florescences terminal, solitary, dense, 12–15 mm; flowers lilac; floral bracts ovate or obovate, 3–3.5 mm long, apex acute or obtuse, slightly strigose. Flower with the calyx 3.5–4.5 mm long, hispid, with 4 brief teeth, unequal, triangular; corolla tube 4–6 mm, with villous fauce. Cluse $2\text{--}3 \times 0.5$ mm, elliptical in cross section, commissural faces not connate.

Iconography. Botta (1980: 518, fig. 1); Caro (1982: 17, fig. 3).

Distribution and habitat. *Aloysia deserticola* grows in northwestern Argentina, southern Bolivia, and Chile, Region II. This species is found at elevations of 2300–3500 m and is noted to occur frequently on rocky to sandy soils.

Discussion. The four species *Aloysia deserticola*, *A. tarapacana* (Botta) Lu-Irving & N. O'Leary, *A. riojana* (Hieron. ex Moldenke) Lu-Irving & N. O'Leary, and *A. salsoloides* (Griseb.) Lu-Irving & N. O'Leary were formerly recognized in *Acantholippia* and have short floriferous branches that develop over the previous year's stems, as stated by Múlgura et al. (2002). In addition, each of these species has erect, imbricate leaves with inverse dorsiventral mesophyll (Carmona & Ancibor, 1995).

Moldenke (1961) mentioned *Verbena deserticola*, described by Philippi (1860), as a synonym of *Acantholippia deserticola*. However, *V. deserticola* is actually a synonym referred to *Junellia origenes* (Phil.) N. O'Leary & P. Peralta (O'Leary et al., 2011).

Selected specimens examined. ARGENTINA. **Catamarca:** Antofagasta de la Sierra, *Ulibarri et al.* 679 (SI). **Jujuy:** Susques, ca. de Olacapato, esquina Azul, *Cabrera et al.* 31792 (SI). **Salta:** Los Andes, camino de Pocitos a Canchari, *Ruthsatz* 213 (SI). **San Juan:** Dpto. Iglesia, Parque Nac. San Guillermo, *E. Haene et al.* 2121 (SI). BOLIVIA. **Oruro:** Atahualpa, al S de Sabaya, salar de Coipasa, *Beck* 21555 (SI). **Potosí:** Nor Lipez, *E. García* 1209 (SI). CHILE. **Region II:** Antofagasta, El Loa, 60 km E ruta 5, on rte. to Solar de Aguas Calientes, *Dillon et al.* 6018 (SI).

10. *Aloysia dusenii* Moldenke, Phytologia 1: 440. 1940. TYPE: Brazil. Paraná: shrubby campo at Tamandré, 4 Oct. 1914, *P. Dusén* 1050a (lectotype, designated by Siedo [2010: 200], S11-10477 not seen, S image!; isolectotype, NY [barcode] NY00103874 not seen, NY image!). Figure 4.

Aloysia ternifolia Moldenke, *Phytologia* 2: 309. 1947. TYPE: Brazil. Paraná: Itaiacoca, Ponta Grossa, 17 Mar. 1904, *P. K. Dusén* 4228 (holotype, S11-10485 not seen, S image!; isotypes, NY [barcode] NY00103891 not seen, NY image!, NY [bc] NY00103892 not seen, NY image!, US [bc] US00118881 not seen, US image!).

Aloysia ternifolia Moldenke f. *oppositifolia* Moldenke, *Phytologia* 28: 192. 1974. TYPE: Brazil. Paraná: Pitanga, rio Bonito, 25 Feb. 1971, *G. Hatschbach* 26516 (holotype, TEX-LL [barcode] LL00374942 not seen, TEX-LL image!; isotypes, SI [bc] SI041146!, UC [bc] UC1426950 not seen, UC image!, US [bc] US00118882 not seen, US image!).

Shrubs 1–2 m tall; stems glabrous. Leaves mostly opposite, sometimes 3-whorled, sessile to subpetiolate, petiole 2–4 mm; blades narrowly elliptic to elliptic, $3\text{--}4$ (–5) \times 1–1.5 cm, apex acute to subobtuse, base acute, margins entire toward base, minutely serrate toward apex, abaxially strigose on midvein, adaxially with adpressed strigose pubescence over entire surface. Florescences axillary, solitary or sometimes 2 per leaf axil, lax, 3–8 cm;

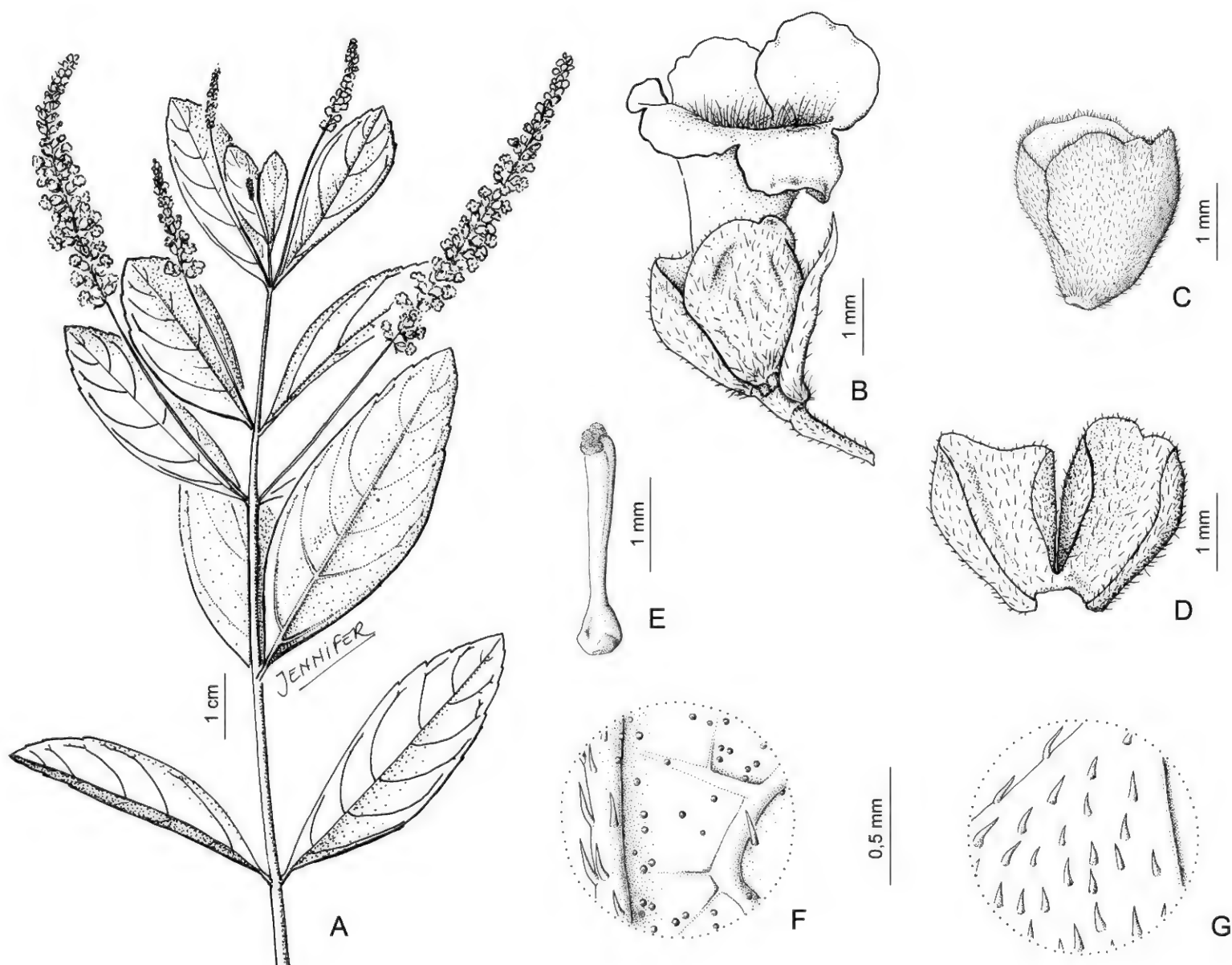


Figure 4. *Aloysia dusenii* Moldenke. —A. Floriferous branch, showing the axillary florescences (homothetic pleiobotrya). —B. Intact flower in lateral view, with floral bract subtending the lightly strigose calyx. —C. Detail of bilobulated calyx. —D. Detail of dissected bilobulated calyx, internal view. —E. Gynoecium. —F. Detail of leaf abaxial surface, strigose on midvein. —G. Detail of leaf abaxial surface, with adpressed strigose pubescence. A–G, taken from *Hatschbach 22546* (SI).

peduncles 1–3.5 cm; flowers white; pedicels 0.2–0.5 mm; floral bracts narrowly elliptic, 2–2.5 mm, apex acute, strigose. Flower with the calyx bilobulated, 2–2.5 mm, lightly strigose; corolla tube 3–4 mm, externally glabrous, with villous fauce. Cluse 1.5×1 mm, glabrous.

Distribution and habitat. *Aloysia dusenii* is endemic to Brazil (Paraná, Rio Grande do Sul, Santa Catarina) and has been observed to grow on riverbanks or on marginal moist forests.

Discussion. *Aloysia dusenii* is remarkable in relation to its bilobulated calyx, which is 4-toothed in the rest of the South American *Aloysia* taxa. Bilobulated calyces are seen among North American *Aloysia* such as *A. coalcomana* Siedo and are frequent within *Lippia*.

Selected specimens examined. BRAZIL. **Paraná:** Guarapuava, Rio Jordao, *Hatschbach 22546* (SI); General Carneiro, faz. dos Souzas, *Hatschbach 28366* (SI). **Rio**

Grande do Sul: Bom Jesus, Pelotas, de S. Joaquim a Ronchinha, *Krapovickas 38344* (SI). **Santa Catarina:** Rio Pelotas, crossing rd. from Silveira to Sao Joaquim, *Olmstead 2010-217* (SI); Mun. Sao Joaquim, Lajes, *Lourteig 2189* (SI).

11. *Aloysia fiebrigii* (Hayek) Moldenke, Revista Sudamer. Bot. 4: 15. 1937. Basionym: *Lippia fiebrigii* Hayek, Bot. Jahrb. Syst. 42: 165. 1909. TYPE: Bolivia. Tarija, 4 Feb. 1904, K. *Fiebrig 3036* (lectotype, designated by Wood [2009: 515], K [barcode] K000470999 not seen, K image!; isoelectotypes, A [bc] A00069310 not seen, A image!, BM [bc] BM000643747 not seen, BM image!, E [bc] E00373278 not seen, E image!, F [bc] F0092410F not seen, F image!, F [bc] F0093491F not seen, F image!, G [bc] G00386442 not seen, G image!, GH [bc] GH00069311 not seen, GH image!, GOET [bc] GOET011516 not seen, GOET image!, M [bc] M0111834 not seen, M image!, NY [bc] NY00137758 not seen, NY image!, P [bc] P00713756 not seen, P image!, P

[bc] P00713757 not seen, P image!, S11-10531 not seen, S image!, S11-10526 not seen, S image!, SI [bc] SI003507!, SI [bc] SI003383!, SI [bc] SI003508!, US [bc] US00118823 not seen, US image!, W 1911-0001742 not seen, W image!).

Aloysia arcuifolia G. L. Nesom, Phytologia 70: 145. 1991. TYPE: Bolivia. Potosi: Valle de Palqui, 7 Feb. 1987, R. Ehrlich 339 (holotype, TEX [barcode] TEX00374932 not seen, TEX image!; isotype, LPB [bc] LPB0000837 not seen, LPB image!).

Shrubs 1–2 m tall. Leaves verticillate, in whorls of 3, sometimes 4, rarely opposite, subsessile; blades linear to elliptic, $1.8\text{--}3 \times 0.2\text{--}0.5$ cm, apex acute, base acute, attenuate, margin entire, adaxially scabrous, abaxially glabrate, with underlayer of glandular trichomes, midvein abaxially conspicuous. Florescences terminal and axillary (heterothetic pleiobotrya), dense, brief, 1–2 cm; peduncles 0.5–1 cm; flowers white; floral bracts ovate, apex acuminate, 2–2.5 mm, lightly strigose, margin ciliate. Flower with the calyx 1.5 mm, strigose, with 4 brief teeth, unequal, triangular; corolla tube 5.5 mm, with glabrous fauce. Cluse 1×0.5 mm, glabrous.

Iconography. Botta (1979: 102, fig. 11).

Distribution and habitat. *Aloysia fiebrigii* has been observed to grow in southern Bolivia and northwestern Argentina (Jujuy, Salta).

Discussion. Siedo (2010) lectotypified this taxon superfluously, because Wood had previously designated the lectotype for *Aloysia fiebrigii* (Wood, 2009).

Aloysia fiebrigii shares with *A. arequipensis*, *A. citrodora*, *A. herrerae*, and *A. velutina* the presence of axillary and terminal florescences, a group of five species in *Aloysia* with heterothetic pleiobotrya. It is distinguished from these species, except from *A. citrodora*, by its ternate leaves, with the leaves being opposite in the rest. *Aloysia citrodora* and *A. fiebrigii* may be differentiated by their leaves, being smaller (blades $1.8\text{--}3 \times 0.2\text{--}0.5$ cm) and with entire margins in the latter, and larger (blades $2\text{--}8 \times 1\text{--}2.5$ cm) and with entire or slightly serrate margins in the former.

Selected specimens examined. ARGENTINA. **Jujuy:** Santa Catalina, Cieneguillas, Arenas 927 (SI). **Salta:** Hunziker 8055 (CORD). BOLIVIA. **Chuquisaca:** entre Muyuquiri y Camargo, Cocucci 3366 (SI). **Tarija:** Yunchará, Rupaska, Beck 26988 (SI); s. loc., s.d., Fiebrig 3040 (SI).

12. *Aloysia gratissima* (Gillies & Hook. ex Hook.) Tronc., Darwiniana 12: 527. 1962. Basionym: *Verbena gratissima* Gillies & Hook. ex Hook.,

Bot. Misc. 1: 160. 1829. TYPE: Argentina. Mendoza, 1829, G. Gillies s.n. (holotype, K [barcode] K000470994 not seen, K image!; isotypes, BM [bc] BM000643772 not seen, BM image!, BM [bc] BM000643773 not seen, BM image!, E [bc] E00320620 not seen, E image!, E [bc] E00320623 not seen, E image!, E [bc] E00320622 not seen, E image!, GH [bc] GH00069316 not seen, GH image!, GH [bc] GH00299005 not seen, GH image!, OXF not seen, SI [bc] SI003701!). Figure 5.

Shrubs 1–3 m tall; stems glabrous, sometimes puberulous when young. Leaves opposite, subsessile, or briefly petiolate to 3 mm, sometimes fasciculate, membranaceous or coriaceous; blades elliptic to ovate, $0.15\text{--}7 \times 0.05\text{--}3$ cm, apex acute or sometimes subobtuse, base acute, margins entire, dentate, or serrate, or basally entire and serrate toward apex, adaxially scabrous, abaxially glabrate to lightly strigose, midvein only impressed on abaxial surface or the venation pinnate, conspicuous. Florescences axillary, solitary, lax, or dense, 3–13 cm; peduncles 0.5–3 cm; flowers white; floral bracts ovate, apex acute, 1–2 mm, lightly strigose, margin ciliate. Flower with the calyx 2–4 mm, hispid in inferior half, lightly hispid toward apex, calyx with 4 teeth, unequal, triangular; corolla tube 3–5 mm, externally puberulous toward apex, with villous fauce. Cluse $1\text{--}2 \times 0.5$ mm, glabrous.

Distribution and habitat. *Aloysia gratissima* is an amply distributed species, growing throughout the Americas. *Aloysia gratissima* var. *gratissima* has the most far-reaching distribution, being the only taxon in the genus that occurs in both South and North America. Its geographic distribution extends from the southwestern United States and northern Mexico, into southern South America. Three other varieties of *A. gratissima* are here recognized (*A. gratissima* var. *schulziana* (Moldenke) Botta, *A. gratissima* var. *angustifolia* (Tronc.) Botta, and *A. gratissima* var. *chacoensis* (Moldenke) Botta) and have distributions restricted to southern South America. Consequently, in South America four varieties of *A. gratissima* are recognized.

Discussion. Ragonese (1955) stated that *Aloysia gratissima* is an aromatic shrub known to be toxic for cattle.

Aloysia gratissima is a problematic taxon, and throughout the years botanists (Troncoso, 1964; Botta, 1979; Siedo, 2006) have differed in the significance of singular characters to delimit this complex, which has been reflected in the variable number of species and

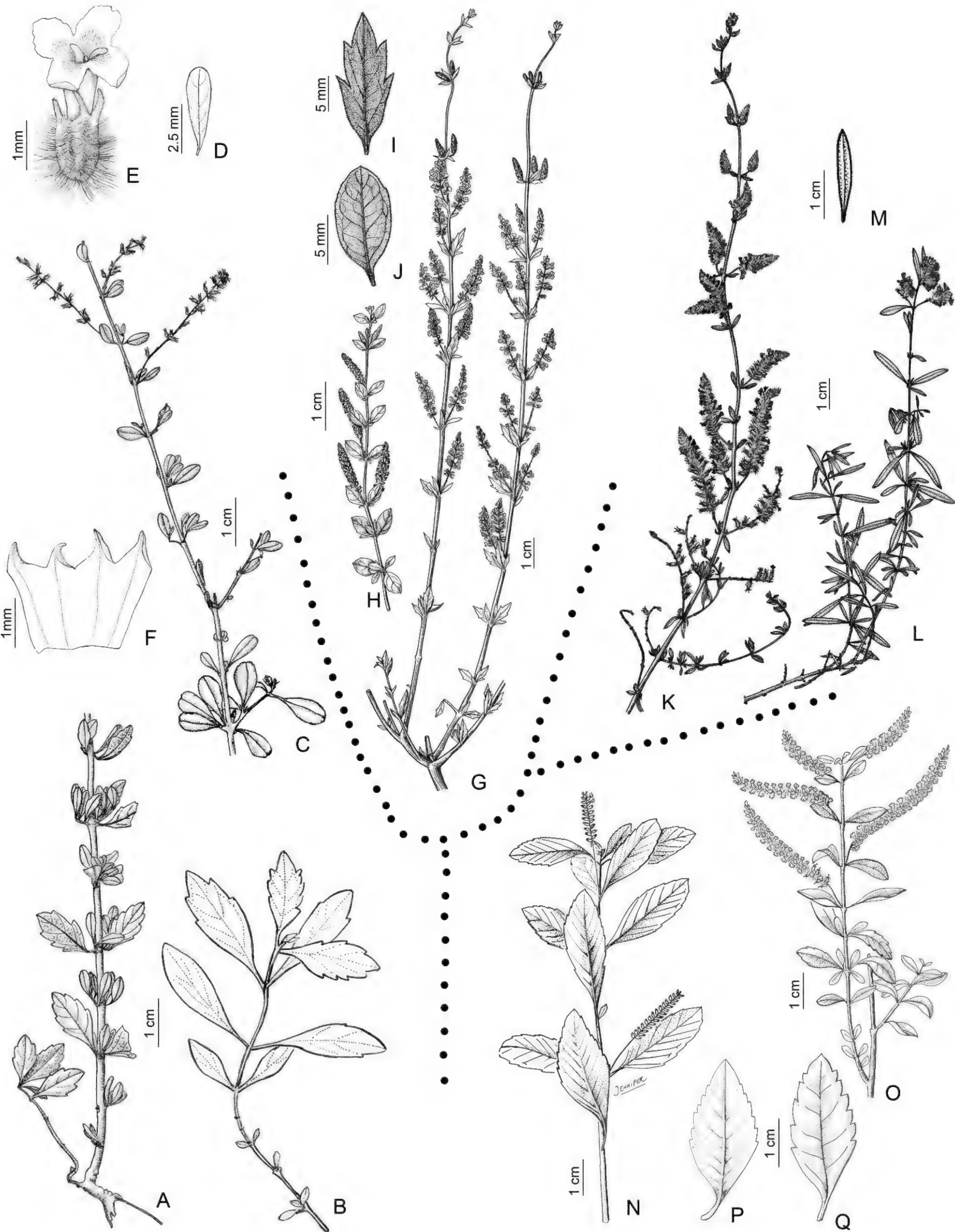


Figure 5. *Aloysia gratissima* (Gillies & Hook.) Tronc. A–F. *Aloysia gratissima* var. *gratissima*. —A. Basal branch. —B. Apical branch. —C. Fructiferous branch. —D. Leaf. —E. Intact flower with calyx hispid in lower half, with three teeth (of four) visible. —F. Dissected calyx, internal view. G–J. *Aloysia gratissima* var. *chacoensis* (Moldenke) Botta. —G. Floriferous branch with dentate leaves. —H. Apical branch with entire leaves. —I. Basal leaf with dentate margin in upper half. —J. Apical leaf with entire margins. K–M. *Aloysia gratissima* var. *angustifolia* (Tronc.) Botta. —K. Fructiferous branch with apical leaves. —L. Floriferous branch with basal leaves. —M. Mature leaf. N–Q. *Aloysia gratissima* var. *schulziana* (Moldenke) Botta. —N. Floriferous branch. —O. Fructiferous branch. —P. Leaf, abaxial surface with conspicuous pinnate venation. —Q. Leaf, adaxial surface. A–F from Schinini 10366 (SI); G–J from Schulz 1494 (holotype, *A. gratissima* var. *chocoensis*, CTES); K from Burkart 23805 (SI); L–M from Burkart 6695 (holotype, *A. gratissima* var. *angustifolia*, SI); N from Krapovickas 30899 (SI); O–Q from Cabrera 14633 (SI).

varieties recognized over time. Lu-Irving et al. (2014) hypothesized that this group may represent a recent radiation, given that branch lengths are short throughout the *A. gratissima* clade. Therefore, a population-level approach to sampling may be required to elucidate the identities and evolutionary histories of taxa belonging to this clade. Recently, Moroni et al. (2016) applied a statistical approach to try to resolve relationships within *A. gratissima*.

Cytology. A mitotic chromosome count of $2n = 54$ has been reported for the species *Aloysia gratissima* (Powell et al., 2010).

TAXONOMIC KEY TO THE VARIETIES OF *ALOYSIA GRATISSIMA*

1. Apical leaf blades small, less than 2 cm long, or small throughout the entire stem axis; florescences dense, 3–7 cm long 2
- 1'. Apical leaf blades larger than lower ones, more than 2 cm long; florescences lax, 5–13 cm long ... 3
2. Leaf blades with entire margins, less than 2 cm long throughout the entire plant
..... 12a. *A. gratissima* (Gillies & Hook. ex Hook.) Tronc. var. *angustifolia* (Tronc.) Botta
- 2'. Leaf blades on upper plant stems with entire margins or sometimes 1- to 3-dentate, blades less than 1 cm long, leaf blades on lower plant stems with 1 to 4 teeth, blades more than 2.5 cm long
..... 12b. *A. gratissima* (Gillies & Hook. ex Hook.) Tronc. var. *chacoensis* Moldenke
3. Leaves with an acute apex and serrate margins; abaxial blades with conspicuous pinnate venation
... 12d. *A. gratissima* (Gillies & Hook. ex Hook.) var. *schulziana* (Moldenke) Botta
- 3'. Leaves with an acute or subobtusate apex and entire margins, sometimes serrate; abaxial blades with only the midvein impressed
... 12c. *A. gratissima* (Gillies & Hook. ex Hook.) Tronc. var. *gratissima*

12a. *Aloysia gratissima* (Gillies & Hook. ex Hook.) Tronc. var. ***angustifolia*** (Tronc.) Botta, Darwiniana 22: 89. 1979. Basionym: *Aloysia chacoensis* var. *angustifolia* Tronc., Darwiniana 13: 630. 1964. TYPE: Argentina. Buenos Aires: Campana, 28 Oct. 1934, A. Burkart 6695 (holotype, SI [barcode] SI003379!; isotype, SI [bc] SI003378!). Figure 5K–M.

Aloysia decipiens Ravenna, Onira 11(4): 14–15. 2007. TYPE: Argentina. Santiago del Estero: Dpto. Robles, colonia Jaime, 19 Nov. 1948, B. Luna Ruiz s.n. (holotype, BA [barcode] BA53388!).

Xerophytic shrubs; leaves small, narrow elliptic, up to 2×0.3 cm, with an acute apex and base, entire

margins, and a conspicuous midvein abaxially. Florescences dense, 3–7 cm long.

Distribution and habitat. *Aloysia gratissima* var. *angustifolia* grows in central Argentina (Buenos Aires, Chaco, Córdoba, Entre Ríos, La Pampa, La Rioja, Santa Fé, and Santiago del Estero) and also in western Paraguay.

Discussion. Ravenna (2007) stated that *Aloysia decipiens* was closely related to *A. beckii* Moldenke; however, this name is treated as a synonym of *A. gratissima* var. *gratissima* herein. Study of the type material of *A. decipiens* evinces that it shares a similar leaf morphology with *A. gratissima* var. *angustifolia*, and therefore Múlgura et al. (2012) considered the species name a synonym of this variety.

Selected specimens examined. ARGENTINA. **Buenos Aires:** Campana, barranca Paraná, Krapovickas 2597 (NY). **Chaco:** Resistencia, Malvarez 1367 (NY). **Córdoba:** Punilla, Villa del Lago, Cabrera et al. 29664 (SI). **Diamante:** Barranca, Burkart 28067 (SI). **Entre Ríos:** Paraná, Paracao, Burkart et al. 23805 (SI). **La Pampa:** Guatraché, Estancia Remecó, Rúgolo 1275 (SI). **La Rioja:** Chilecito, Meyer 4087 (NY). **Santa Fé:** General Obligado, Villa Ana, Villa Ocampo, Ragones 3120 (SI). **Santiago del Estero:** San Martín, ruta 34, Km. 571, Aliscioni et al. 692 (SI). **Tucumán:** s.d., D. Cozzo s.n. (NY). PARAGUAY. **Boquerón:** Colonia Menno, Arenas 1085 (SI). **Chaco:** Loma Porá, Rojas 2542 (SI).

12b. *Aloysia gratissima* (Gillies & Hook. ex Hook.) Tronc. var. ***chacoensis*** (Moldenke) Botta, Darwiniana 22: 89. 1979. Basionym: *Aloysia chacoensis* Moldenke, Lilloa 5: 373. 1940. TYPE: Argentina. Chaco: Tirol, on side of mtn., Feb. 1934, A. G. Schulz 1494 (holotype, NY [barcode] NY00103873 not seen, NY image!; isotype, CTES [bc] CTES0013810 not seen, CTES image!). Figure 5G–J.

Aloysia casadensis Hassl. ex Moldenke, Phytologia 3: 106–107. 1949. TYPE: Paraguay. Puerto Casado, Feb. 1917, T. Rojas 2529 (holotype, MVM not seen; isotypes, NY [barcode] NY00103869 not seen, NY image!, NY [bc] NY00103868 not seen, NY image!, SI [bc] SI003388!).

Leaves small, elliptic, with lengths of less than 1 cm toward apical portion of plant stems, but lengths to 4 cm with 1 to 4 teeth, toward basal portions. Florescences dense, 3–7 cm long.

Distribution and habitat. Most specimens of *Aloysia gratissima* var. *chacoensis* grow in the Argentinean provinces of Chaco and Formosa. This variety is less commonly found in Santa Fé, Santiago del Estero, and Córdoba, and also occurs in western Paraguay.

Selected specimens examined. ARGENTINA. **Chaco:** Enrique Urién, *Schulz* 772 (NY); Pampa del Infierno, *Meyer* 5066 (NY). **Córdoba:** Ischilín, Dean Funes a San Vicente, *de la Sota* 198 (NY). **Formosa:** Camino de Fortín Nuevo, Pilcomayo a La Esmeralda, *Cordini* 60 (SI). **Santa Fé:** San Bernardo, *Alonso* 548 (SI). **Santiago del Estero:** Espada, *Argañarás* 61 (SI). PARAGUAY. **Alto Paraguay:** Puerto Casado, *Rojas* 7701 (SI). **Boquerón:** Colonia Fernheim, Filadelfia, *Arenas* 1879 (SI). **Presidente Hayes:** Ea. Loma Pyta, *Arenas* 664 (SI).

12c. *Aloysia gratissima* (Gillies & Hook. ex Hook.)
Tronc. var. ***gratissima***. Figure 5A–F.

Aloysia lycioides Cham., *Linnaea* 7: 237. 1832. *Lippia lycioides* (Cham.) Steud., *Nomencl. Bot.* [Ed. 2] 2: 62. 1841. TYPE: Brazil meridian, s.d., *F. Sellow s.n.* (lectotype, designated by Múlgura et al. [2012: 17], K [barcode] K000487005 not seen, K image!, K; isoelectotypes, BM [bc] BM001118329 not seen, BM image!, BR [bc] BR0000005720156 not seen, BR image!, HAL [bc] HAL0107063 not seen, HAL image!, HAL [bc] HAL0107062 not seen, HAL image!, K [bc] K000487006 not seen, K image!, G [bc] G00386444 not seen, G image!, M [bc] M0111831 not seen, M image!, NY not seen, NY photo at SI!, US [bc] US01049793 not seen, US image!, SI [bc] SI003390!, SI [bc] SI003391!).

Aloysia floribunda M. Martens & Galeotti, *Bull. Acad. Roy. Sci. Bruxelles*, 11(2): 320. 1844, syn. nov. TYPE: Mexico. Veracruz: June–Oct. 1840, *H. Galeotti* 774 (holotype, BR [barcode] BR005187300 not seen, BR image!).

Lippia ligustrina (Lag.) Britton var. *lasiodonta* Briq., *Annuaire Conserv. Jard. Bot. Genève* 7–8: 305. 1904. TYPE: Paraguay. Paraguarií, 15 Mar. 1881, *B. Balansa* 3117 (holotype, G [barcode] G00166265 not seen, G image!; isotypes, BM [bc] BM000643660 not seen, BM image!, GH [bc] GH00299001 not seen, GH image!, F [bc] F0092411F not seen, F image!, K [bc] K000487007 not seen, K image!, SI!).

Lippia ligustrina (Lag.) Britton var. *paraguariensis* Briq., *Annuaire Conserv. Jard. Bot. Genève* 7–8: 305. 1904. *Aloysia ligustrina* var. *paraguariensis* (Briq.) Moldenke, *Phytologia* 1: 167. 1935. *Aloysia lycioides* var. *paraguariensis* (Briq.) Moldenke, *Phytologia* 2: 464. 1948. *Aloysia gratissima* (Gillies & Hook.) Tronc. var. *paraguariensis* (Briq.) Moldenke, *Phytologia* 9: 500. 1964. TYPE: Paraguay. Paraguarií, Jan. 1875, *B. Balansa* 1015 (holotype, G [barcode] G00166413 not seen, G image!; isotypes, BR not seen, BR photo at SI!, G [bc] G00166414 not seen, G photo at SI!, G image!, SI-67609!).

Aloysia beckii Moldenke, *Phytologia* 52(1): 18. 1982. TYPE: Bolivia. Cochabamba: Carrasco, Cochabamba hacia Santa Cruz, 27 Sep. 1981, *S. Beck* 7036 (holotype, TEX-LL [barcode] LL00374934 not seen, TEX-LL image!; isotypes, LPB [bc] LPB0000839 not seen, LPB image!, M [bc] M0112713 not seen, M image!, SI [bc] SI003374!).

Aloysia famatinensis Ravenna, *Onira* 11(4): 15–16. 2007. TYPE: Argentina. La Rioja: Sierra de Famatina, Guanchín Viejo, 25 Jan. 1928, *A. Castellanos s.n.* (holotype, BA-28328!).

Leaves elliptic to ovate, generally glabrate, with an acute to subobtuse apex and blade margins entire, sometimes slightly serrate; abaxial blade surface with only the midvein impressed. Florescences lax, 5–13 cm long.

Distribution and habitat. *Aloysia gratissima* var. *gratissima* is amply distributed across northern, northeastern, and northwestern Argentina, extending south to La Pampa. The autonymic variety also occurs in Chile, Bolivia, Paraguay, Uruguay, and southern Brazil. It is found across northern Mexico and in the southwestern United States. This is the only taxon of *Aloysia* known to occur in both South and North America, with an interesting distributional disjunction between northern populations (southwestern United States and adjacent Mexico) and southern ones (Brazil and south). *Aloysia gratissima* var. *gratissima* has been collected and noted as frequent along riverbanks or in xeromorphic scrublands.

Discussion. In northeastern Corrientes Province, Argentina, as well as Paraguay, a phenotype exists (*Morel* 1257 [NY]; *Jorgensen* 2473 [NY]) that has slightly obovate or rounded leaves, with an entire margin and obtuse apex, with a prominent midvein abaxially and multiple fasciculate leaves at stem nodes. This resembles what Moldenke (1935) referred to as *Aloysia ligustrina* var. *paraguariensis*, which is herein considered a synonym of *A. gratissima* var. *gratissima*.

Study of the type material of *Aloysia floribunda* indicates that this species is the same taxon as *A. gratissima* var. *gratissima*. This was first proposed by Múlgura et al. (2012), given that the type specimen has lax florescences longer than 5 cm, with leaves with a subobtuse apex and entire margin. Wood (2009) mentioned that the holotype of *A. lycioides* was housed at LE, but none of the authors have seen it. A lectotype was selected by Múlgura et al. (2012) from a specimen housed at K.

Selected specimens examined. ARGENTINA. **Buenos Aires:** Campana, *Burkart* 3083 (SI). **Catamarca:** Tinogasta, cuesta de Zapata, *Cabrera* 24648 (SI). **Chaco:** Colonia Benítez, *Schulz* 8317 (SI). **Córdoba:** Punilla, Los Gigantes, *Sayago* 940 (SI). **Corrientes:** Santo Tomé, Arroyo Chimiray, Río Uruguay, *Schinini* 10366 (CTES; SI). **Curuzú Cuatiá:** Est. María Azucena, *Schinini* 13902 (SI). **Entre Ríos:** Concordia, Salto Grande, *Cabrera* 19245 (SI). **Formosa:** s. loc., *Jörgensen* 2473 (NY). **Jujuy:** Tumbaya, Volcán, Laguna, *Burkart* 30608 (SI). **La Pampa:** Sierra de Lihuel Calel, 30 Nov. 1959, *Troncoso s.n.* (SI 20589). **La Rioja:** Chilecito, Quanchín, *Okada* 2747 (SI). **Mendoza:** Tunuyán, *Ruiz Leal* 1102 (SI). **Misiones:** Caingúas, rte. 7, camino de Aristóbulo del Valle a Jardín América, *Morrone* 635 (SI). **Patiño:** Las Lomitas, 3–5 km SO por rte. 81, *Schinini* 24130 (SI). **Pilcomayo:** Clorinda, *Morel* 1257 (NY). **Salta:**

Anta, finca Pozo Largo, *Saravia Toledo* 716 (SI). **San Juan:** Valle Fértil, Sa. De Valle Fértil, *Kiesling* 4954 (SI). **San Luis:** La Capital, San Martin del Alto Negro, *L. Anderson* 1521 (SI). **Santa Fe:** Garay, entre Santa Rosa y Cayastá, *Ragonese* 2829 (SI). **Santiago del Estero:** Ojo de Agua, *Fabris* 2729 (SI). **Tucumán:** Tafí del Valle, *Schulz* 11465 (SI). BOLIVIA. **Chuquisaca:** Luis Calvo, clausura El Huare, *Saravia Toledo* 11830 (SI). **Cochabamba:** Mizque, canton Molinero, *Sigle* 137 (SI). **Santa Cruz:** Samaipata, *Steinbach* 8248 (NY). **Tarija:** de Tarija a Narvaez, *Kiesling* 3708 (SI). BRAZIL. **Rio Grande do Sul:** Alegrete a Uruguayana, *Nicora* 4726 (SI). CHILE. **Region V:** Limache, *Garaventa* 7092 (SI). ECUADOR. **Pichincha:** Quito, Parque Italia, Barrio Las Casas, *Cerón* 12387 (SI). MEXICO. **Chihuahua:** Bachimba canyon, 23 Mar. 1885, *Pringle s.n.* (SI). **Guanajuato:** 60 mi. S San Luis Potosi, *Dunn* 20552 (MO). **Nuevo Leon:** valley near Monterey, 31 Aug. 1903, *Pringle s.n.* (SI). PARAGUAY. **Boquerón:** Colonia Menno, Lolita, *Vanni* 1830 (SI). **Chaco:** Santa Elisa, *Hassler* 2635 (SI). **Cordillera:** San Bernardino, *Hassler* 53 (SI). **Guaira:** Cordillera de Ybytyruzú, Cerro. Polilla, *Zardini* 8599 (SI). **Itapúa:** Villa Encarnación, *Rojas* 7902 (SI). **Paraguarí:** de Paraguarí a Escobar, *Múlgura* 3743 (SI). **San Pedro:** Alto Paraguay, Primavera, *Woolston* 794 (NY). U.S.A. **Texas:** Jim Hogg Co., NE Hebronville, *Lundell* 11958 (SI). URUGUAY. **Artigas:** Tomás Gomensoro, *Marchesi* 10078 (SI). **Minas:** Arroyo Aguas Blancas, *Crespo* 26457 (SI). **Paysandú:** Arroyo Negro, *Rosengurtt* 2245 (SI). **Rivera:** rte. 29, pasando Minas de Corrales, *Denham* 333 (SI). **Tacuarembó:** *Cabrera* 32345 (SI).

12d. *Aloysia gratissima* (Gillies & Hook. ex Hook.)

Tronc. var. **schulziana** (Moldenke) Botta, Darwiniana 22: 87. 1979. Basionym: *Aloysia schulziana* Moldenke, Lilloa 5: 381. 1940. TYPE: Argentina. Salta: Colonia San Bernardo, Feb. 1936, *A. G. Schulz* 1447 (holotype, NY [barcode] NY00103887 not seen, NY image!; isotypes, CTES [bc] CTES0013830 not seen, CTES image!, SI [bc] SI003394!) Figure 5N–Q.

Aloysia meyeri Moldenke, Lilloa 5: 378. 1940. TYPE: Argentina. Tucumán: Trancas, San Pedro de Colalao, 4 ene. 1940, *T. Meyer* 3092 (holotype, NY [barcode] NY00103881 not seen, NY image!; isotypes, LIL [bc] LIL001365 not seen, LIL image!, SI [bc] SI003389!).

Aloysia looseri Moldenke, Lilloa 5: 377. 1940. *Lippia looseri* (Moldenke) Looser, Revista Univ. (Santiago) 26(2): 141. 1941. TYPE: Chile. Santiago, 15 Dec. 1925, [cult.] *G. Looser* 4008 (holotype, NY [barcode] NY00103879 not seen, NY image; isotypes, SI!, SGO not seen).

Aloysia lomaplatae Ravenna, Onira 10(19): 60. 2006. TYPE: Paraguay. “In scopulosis ad Loma Plata, civit. Boquerón,” 13 Sep. 2001, *P. Ravenna* 5030 (holotype, FCQ not seen).

Leaves elliptic, with an acute apex and serrate margin; blades with pinnate venation conspicuous on abaxial surface. Florescences lax, longer than 5 cm.

Distribution and habitat. The greatest number of specimens attributed to *Aloysia gratissima* var. *schulziana* were collected from northwestern Argenti-

na (Jujuy, Salta). This variety is also known, but less frequently, from the Argentinean provinces of Catamarca, Chaco, Formosa, La Rioja, Misiones, San Juan, and Tucumán. *Aloysia gratissima* var. *schulziana* is also present in southern Bolivia and Paraguay.

Discussion. *Aloysia gratissima* var. *schulziana* is distinguished by its leaves with serrate margins and conspicuous pinnate venation on the abaxial blade surface, with the margins entire or slightly serrate toward apex. Only the midvein is impressed in the other three varieties.

Moldenke (1940) mentioned that type material of *Aloysia looseri* was a specimen cultivated in Chile. The species name is herein considered a synonym of *A. gratissima* var. *schulziana*. Chile is not considered as part of the natural distributional range for *A. gratissima* var. *schulziana*. Elsewhere, this variety is sometimes cultivated for ornamental purposes, as in the suburbs of Buenos Aires.

Ravenna (2006: 60) stated in the protologue of *Aloysia lomaplatae* Ravenna that the species can be distinguished by its “relatively large, somewhat scabrous, conspicuously lobulate-dentate blades.” These are characters that define the variety, and consequently the species name is here considered a synonym of *A. gratissima* var. *schulziana*.

Selected specimens examined. ARGENTINA. **Catamarca:** Ancasti, entre Ancasti e Icaño, *Troncoso* 1824 (SI). **Chaco:** 1° de Mayo, Colonia Benítez, *Schulz* 8699 (SI). **Córdoba:** Quilino, *Cordo* 77-d-45 (SI). **Corrientes:** Ituzaingó, camino a San Carlos, *Krapovickas* 17970 (SI). **Formosa:** Matacos, Ingeniero Juarez, 3 km al S del pueblo, sobre la rte. que va al Bermejo, a Belgrano, *Arenas* 2330 (SI); Patiño, Las Lomitas, *Maranta* 1104 (BA). **Jujuy:** Santa Bárbara, *Cabrera* 31018 (S); entre San Pedro y Santa Clara, *Cabrera* 14633 (SI). **La Rioja:** Independencia, rte. 79, *Pensiero* 7426 (SI). **Misiones:** Posadas, *Bertoni* 761 (NY). **Salta:** Anta. San Javier (8 km al Sud de I.V. González), 1988, *Saravia Toledo* 1750 (SI). **San Juan:** Valle Fértil, Ruta prov. 42, entre San Agustín de Valle Fértil y Las Tumanas, a 23 km del primero, *Biurrun* 4002 (SI). **San Martín:** Río Seco, *Krapovickas* 30899 (SI). **Santiago del Estero:** Choya, *Sayago* 2649 (SI). **Tarija:** Villa Montes, Abra de Tapequa, *Krapovickas* 19210 (SI). **Tucumán:** Leales, La Florida, *Krapovickas* 17337 (SI). BOLIVIA. **Potosí:** Nor Chichas, Aripalca, 10 Mar. 1993, *Torrico* 107 (SI). **Tarija:** Villa Montes, Abra de Tapequa, 25 May 1971, *Krapovickas* 19210 (SI). PARAGUAY. **Boquerón:** s. loc., *Vanni* 2410 (SI).

13. *Aloysia hatschbachii* Moldenke, Phytologia 18(6): 341. 1967. TYPE: Brazil. Paraná: Pien, 8 Mar. 1967, *G. Hatschbach* 16101 (holotype, NY [barcode] NY00103876 not seen, NY image!; isotypes, MO-2217903 not seen, MO image!, TEX-LL [bc] LL00374938 not seen, TEX-LL image!, TEX-LL [bc] LL00374939 not

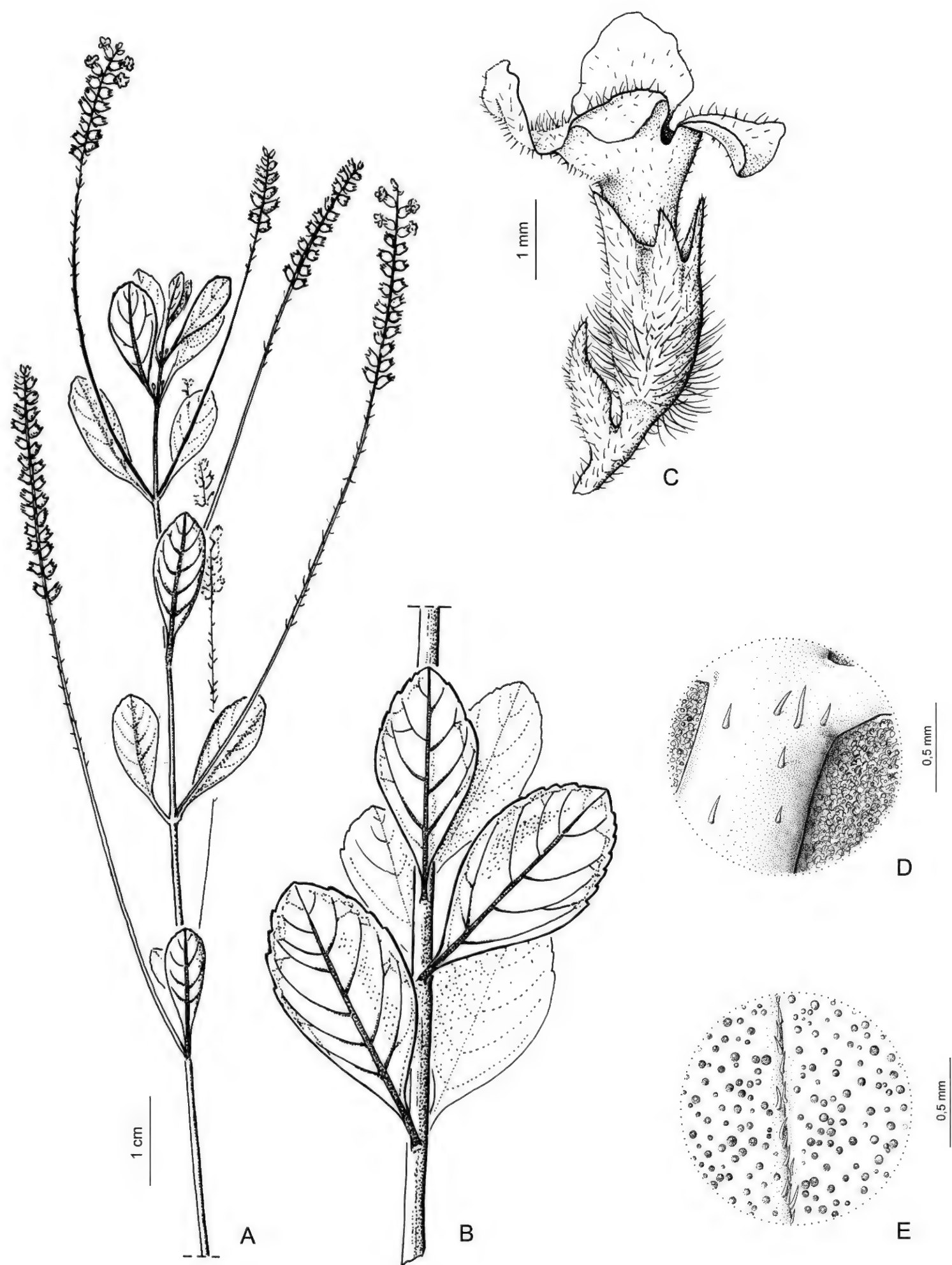


Figure 6. *Aloysia hatschbachii* Moldenke. —A. Floriferous branch, general aspect, with axillary florescences (homothetic pleiobotrya). —B. Detail of branch, showing elliptic leaves with serrulate margins in upper half. —C. Intact flower with hispid calyx subtended by strigose floral bract (at left). —D. Close-up of abaxial leaf surface, glabrous with lightly strigose midvein. —E. Close-up of adaxial leaf surface, glabrous with glandular papillae. A, illustrated from *Hatschbach 16101* (isotype, SI); B–E from *Hatschbach 51897* (SI).

seen, TEX-LL image!, UC [bc] UC1414074 not seen, UC image!, US [bc] US01049795 not seen, US image!, SI [bc] SI041045!, SI [bc] SI003385!, SI [bc] SI003384!, WIS [bc] WIS0255184 not seen, WIS image!). Figure 6.

Shrubs 1–2 m tall; stems glabrous. Leaves opposite, subcoriaceous, briefly petiolate, petiole 2–4 mm; blades elliptic, $2\text{--}3 \times 1\text{--}1.5$ cm, apex subobtuse to obtuse, base acute, decurrent, margins entire toward base, serrulate in upper half, adaxially glabrous, with glandular papillae, abaxially glabrous, scarcely strigose over abaxial midvein, with venation conspicuous, reddish brown, impressed on abaxial surface. Florescences axillary, solitary, lax, 3–8 cm; peduncles 1–4 cm; flowers white to lilac; pedicels 1 mm; floral bracts reduced, narrowly elliptic, 1–1.2 mm, strigose, apex acute. Flower with the calyx 2–3 mm, hispid, with 4 brief teeth, unequal, triangular; corolla tube 3–4 mm, externally glabrate, with villous fauce. Cluse 1.5×1 mm, glabrous.

Distribution and habitat. *Aloysia hatschbachii* is endemic to Brazil (Paraná), where it has been noted to grow in rocky soils.

Discussion. *Aloysia hatschbachii* shares with *A. salviifolia* and varieties of *A. gratissima* the presence of leaf margins with some degree of serration or dentition, but they are always basally entire. *Aloysia hatschbachii* is readily recognized by its conspicuous, reddish brown, impressed pinnate venation on the abaxial surface of the leaf blades.

Selected specimen examined. BRAZIL. **Paraná:** Pien, *Hatschbach 51897* (SI, US).

14. *Aloysia herrerae* Moldenke, *Phytologia* 2: 10. 1941. TYPE: Peru. Urubamba valley, July 1927, *F. L. Herrera 1534* (holotype, F [barcode] F0043367F not seen, F image!; isotype, NY [bc] NY00103877 not seen, NY image!, SI!). Figure 7.

Aloysia ayacuchensis Moldenke, *Phytologia* 6(6): 256, 323. 1958, syn. nov. TYPE: Peru. Ayacucho, *J. J. Soukup 4187* (holotype, NY [barcode] NY00103866 not seen, NY image!).

Shrubs 1–2.3 m tall; stems glabrous. Leaves opposite, sometimes ternate, subsessile or briefly petiolate, petioles 1–5 mm; blades subcoriaceous, narrowly elliptic, $2\text{--}5.5 \times 0.4\text{--}1.5$ cm, apex subobtuse, base obtuse, margins entire, adaxially glabrous or with scattered scabrid hairs, especially along midvein, abaxially scabrid with glandular trichomes and prominent midvein. Florescences terminal and axillary (heterothetic pleiobotrya),

dense, 1–3 cm; peduncles 1 cm; flowers white, cream with pink to violet tube; pedicels 0.5 mm; floral bracts reduced, widely ovate, 2–2.5 mm, apex acuminate, with scarce scabrous pubescence. Flower with the calyx 2–3 mm, with underlayer of sessile glandular trichomes, and scarce scabrous pubescence, calyx with 4 brief acuminate teeth; corolla tube 3–5 mm, strigose on both surfaces. Cluses 1.5×1 mm, glabrous.

Distribution and habitat. *Aloysia herrerae* grows in Peru and Bolivia and has been collected from hillsides, rocky slopes, or open sunny areas. It has been found at elevations up to 2800 m.

Discussion. *Aloysia herrerae* is an aromatic plant, the leaves of which are used to treat headaches. The species is distinguished by its terminal florescences, which are also present in *A. citrodora* and *A. fiebrigii*, with these three taxa sharing heterothetic pleiobotrya. However, *A. herrerae* is differentiated by its opposite leaves, in contrast to the verticillate leaves seen in *A. citrodora* and *A. fiebrigii*. Terminal florescences are also present in *A. velutina* and *A. arequipensis*, but these two species lack entire leaf margins, while the leaf margin is consistently entire in *A. herrerae*. Leaves are serrulate in the upper portion of the blade in *A. arequipensis* but crenate in *A. velutina*.

The type specimen of *Aloysia ayacuchensis* was observed to have both terminal and axillary florescences and opposite leaves. These are both characters that define *A. herrerae*, so the species name is here considered a synonym of the latter.

Selected specimens examined. BOLIVIA. **Chuquisaca:** Zudañez, 5 km from Candelaria toward Icla, *Wood 14658* (K). PERU. **Ancash:** Huaraz, baños de Chancos, *Sanderman 4612* (F, US). **Ayacucho:** Ayacucho, *Ochoa 710* (NY, SI); s. loc., *Soukup 5467* (US). **Cajamarca:** San Miguel, Niepos, *Llatas Quiroz 1513* (SI). **Cuzco:** Calca, *C. Vargas 248* (NY, SI); Urubamba, Chincheros, *Davis 1757* (F, K, NY); Urubamba, Huallabamba, *Olmstead 2009-30* (SI, WTU); Huayocari to Yabncocha, *Núñez 7018* (F). **Huancavelica:** Tayacaja, betw. Izcuchaca & Acostambo, *Hutchison 4199* (NY, SI, US).

15. *Aloysia oblanceolata* Moldenke, *Phytologia* 3: 108. 1949. TYPE: Paraguay. San Bernardino, 1915, *T. Rojas 53a* (holotype, NY [barcode] NY00103883 not seen, NY image!; isotypes, MVM not seen, SI [bc] SI003407!). Figure 8.

Aloysia gratissima (Gillies & Hook. ex Hook.) Tronc. var. *oblanceolata* Moldenke, *Phytologia* 15: 462. 1968, syn. nov. TYPE: Brazil. Rio Grande do Sul: Gloria, SE of Porto Alegre, 2 Oct. 1948, *A. L. Moldenke 19684* (holotype, NY [barcode] NY00103875 not seen, NY image!).

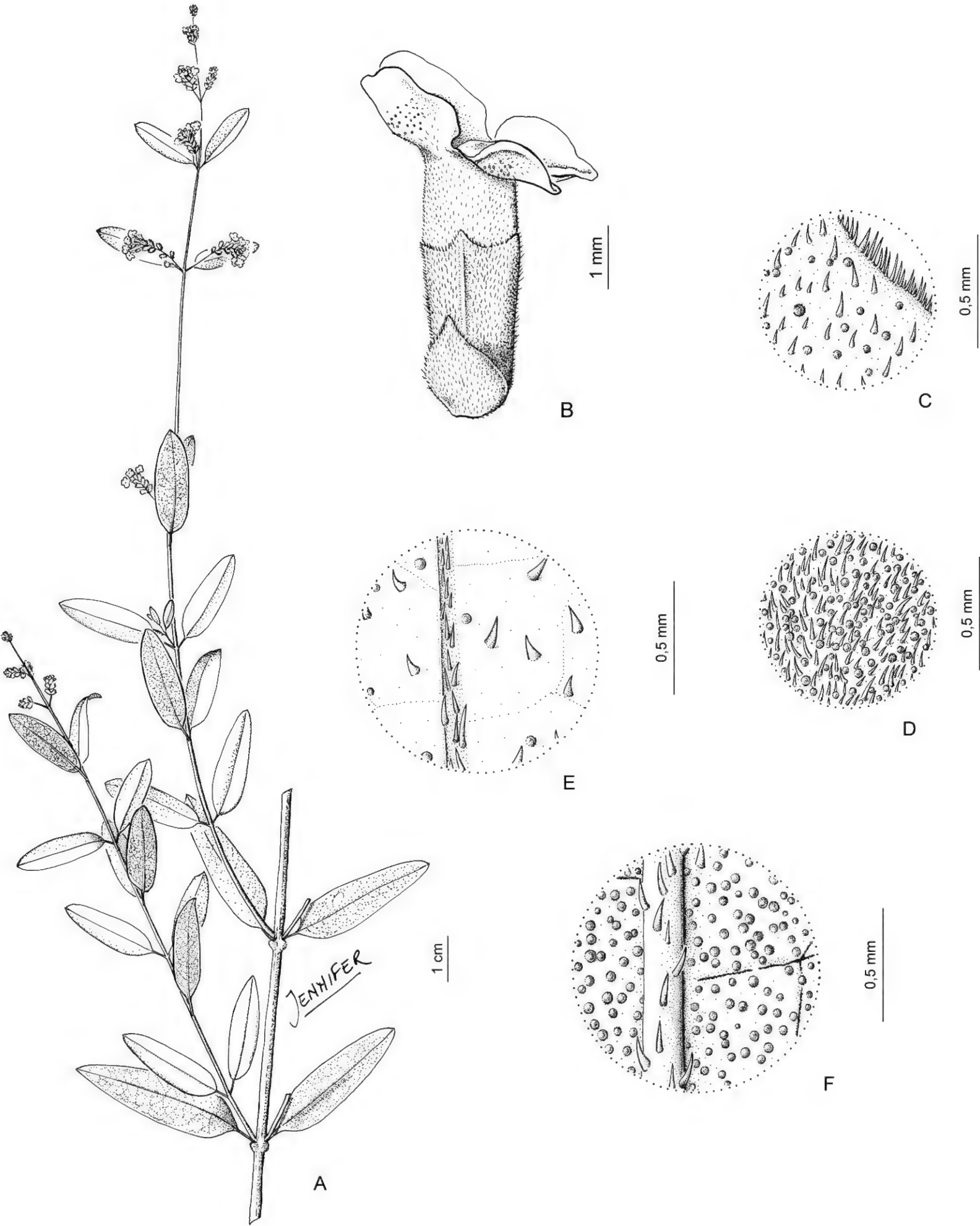


Figure 7. *Aloysia herrerae* Moldenke. —A. Fertile branch, with florescences in both axillary and terminal positions (heterothetic pleiobotrya). —B. Intact flower subtended by widely ovate floral bract. —C. Close-up of floral bract surface, with scattered scabrid hairs and ciliate margins and underlayer of sessile glandular trichomes. —D. Close-up of external calyx surface, scabrid, with underlayer of glandular trichomes. —E. Close-up of adaxial leaf surface, with scattered scabrid hairs, especially along midvein. —F. Close-up of abaxial leaf surface, scabrid with glandular trichomes and prominent midvein. A–F, illustrated from *Olmstead 2009-30* (SI).

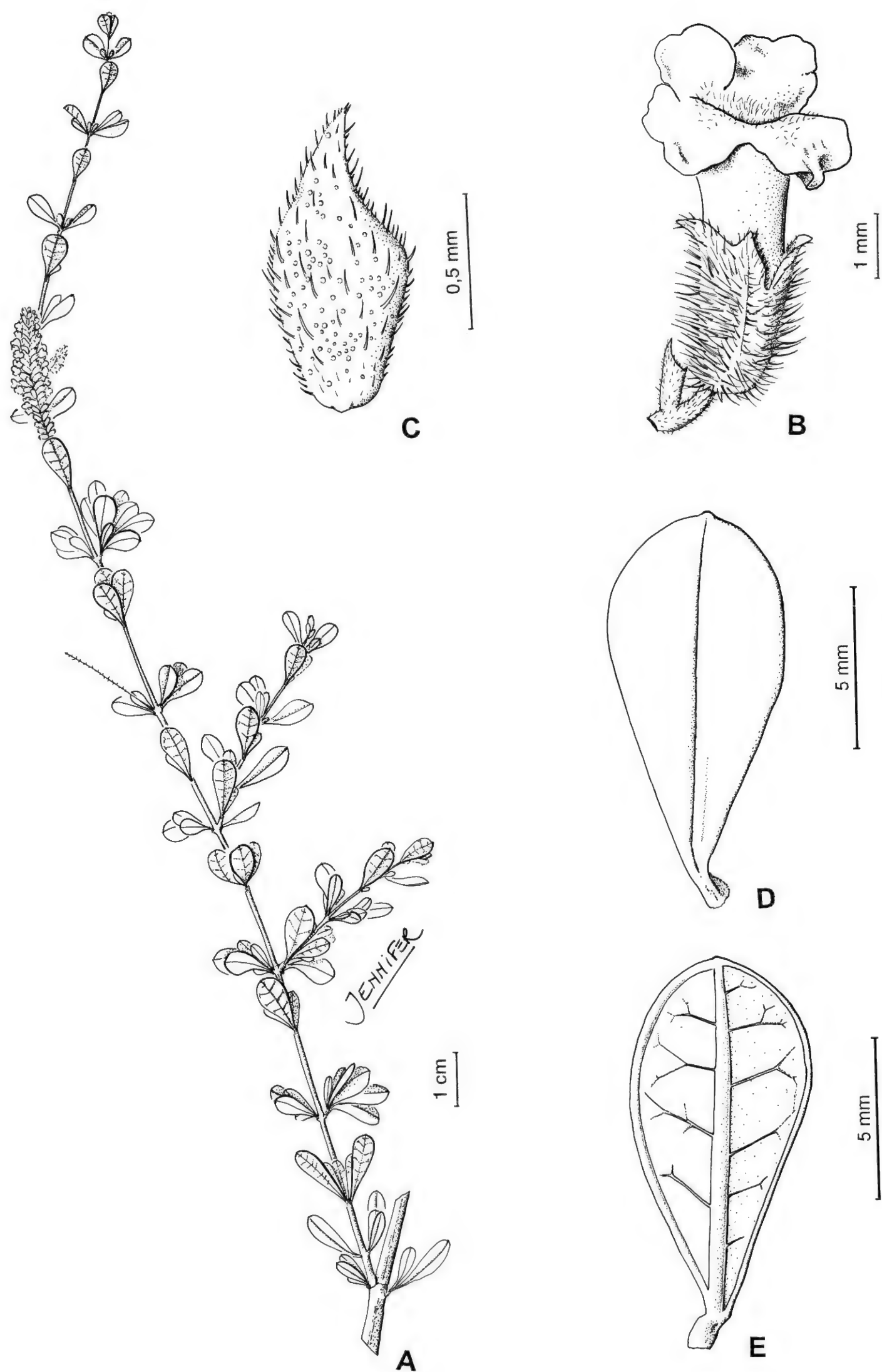


Figure 8. *Aloysia oblanceolata* Moldenke. —A. Fertile branch, general aspect. —B. Flower with hispid calyx and subtending strigose bract (left). —C. Floral bract with ovate, acute apex. —D. Adaxial glabrous leaf surface. —E. Abaxial leaf surface, with prominent midvein and revolute margins. A–E, illustrated from Arenas 148 (SI).

Shrubs 1–2 m tall; stems glabrous. Leaves opposite, generally clustered into fascicles of 4 to 8 leaves, blades sessile, obovate to oblanceolate, $2(-3) \times 0.4$ – 0.6 cm, apex obtuse to round, base acute, attenuate, margins entire, revolute to subrevolute, coriaceous, adaxial surface glabrous, with conspicuous midvein both adaxially and abaxially. Florescences axillary, solitary, dense, 2–5 cm; peduncles 1–2 cm long; flowers white; pedicels 0.5 mm; floral bracts widely ovate, 1–1.5 mm, apex acute, strigose. Flower with the calyx 2–3 mm, hispid, with 4 teeth, unequal, triangular; corolla tube 3–4 mm, glabrate externally, glabrous inside. Cluses 1.5×1 mm, glabrous.

Distribution and habitat. *Aloysia oblanceolata* grows in Paraguay, Bolivia, and Brazil, and is collected from shrubby forests or rocky soils.

Discussion. *Aloysia oblanceolata* is similar to varieties of *A. gratissima*, sharing a leaf morphology with blades that can be elliptic with a subobtuse apex, acute base, and entire margin. *Aloysia oblanceolata* may be distinguished by its fasciculate leaves (vs. not fasciculate in *A. gratissima*) and its revolute to subrevolute blade margins (vs. blade margins not revolute in *A. gratissima*).

Upon examination, the type material of *Aloysia gratissima* var. *oblanceolata*, later described by Moldenke in 1968, is undistinguishable from *A. oblanceolata*, also described by Moldenke in 1949. Thus, this varietal name is here considered a synonym of *A. oblanceolata*.

Selected specimens examined. BOLIVIA. **Cochabamba:** Quillacollo, 22 km hacia Oruro, *Beck* 874 (SI). **Santa Cruz:** Florida, 13 km W Samaipata, *Ferrucci et al.* 2659 (SI). BRAZIL. **Paraná:** Guarapuava, rio Cavernoso, *Hatschbach* 9339 (SI). **Rio Grande do Sul:** Rambo 49976 (SI). PARAGUAY. **Central:** Yparacay, *Hassler* 11497 (NY). **Cordillera:** Caacupé, *Soria* 2098 (NY); Itaugua, cantera, *Arenas* 148 (SI).

- 16. *Aloysia ovatifolia*** Moldenke, *Lilloa* 5: 379. 1940. *Xeroaloyisia ovatifolia* (Moldenke) Tronc., *Darwiniana* 12: 51. 1960. TYPE: Argentina. Córdoba: San Javier, La Barranca, 6 Feb. 1939, *A. Castellanos s.n.* (holotype, NY [barcode] NY00103884 not seen, NY image!; isotypes, BA!, CORD [bc] CORD00003824 not seen, CORD image!).

Shrubs small, 0.5–0.75(–1.2) m tall; stems densely puberulent when young, glabrescent in age. Leaves opposite, sometimes clustered into fascicles, petioles 0.2–1 cm; blades ovate to deltate, 1.5 – 5×1 – 3 cm, apex subobtuse, base truncate, margins coarsely crenate, adaxially hispid, abaxially strigose, pinnate

and reticulate venation prominent on abaxial surface. Florescences axillary, solitary, dense, 2.5–10 cm, elongating to 20 cm in fructification; peduncles 1–2 cm; flowers in whorls of ca. 5, white to pinkish white; pedicels 0.5 mm, floral bracts ovate, 2.5–4 mm, apex acute, strigose. Flowers with the calyx 3 mm, hispid, with long hairs on nerves, with 4 teeth, unequal, triangular; corolla tube 3–4 mm, externally glabrous, with villous fauce. Fruit undivided, drupaceous, obovoid, covered by the acrescent calyx, 2 – 2.5×1.5 – 2 mm, with two 1-seeded locules.

Iconography. Troncoso (1960: 52, fig. 1, 53, fig. 2, 55, fig. 3).

Distribution and habitat. *Aloysia ovatifolia* is endemic to northwestern Argentina where it is found on rocky slopes, in sunny, sandy, dry soils.

Discussion. *Aloysia ovatifolia* is unique in *Aloysia* in having fruits undivided and drupaceous, being schizocarpic in the rest of the taxa. It also can be differentiated by its blades ovate to deltate, with subobtuse apex, truncate base, and margins coarsely crenate.

Selected specimens examined. ARGENTINA. **Catamarca:** Tinogasta, rte. 45, 14 km N Tinogasta, *J. Hunziker* 11998 (SI). **Córdoba:** Sobremonte, San Francisco del Chañar, *Burkart* 29641 (SI). **La Rioja:** General Belgrano, entre Nepe y Los Baldes, *Riedel* 226 (SI). **Mendoza:** San Carlos, rte. 1001, 6 km S jct. rte. 40, *Olmstead* 2001-184 (SI). **San Juan:** Valle Fértil, ceros rodean Embalse, *Roig* 8424 (SI). **San Luis:** Belgrano, Estancia El Médano, 65 km NO de San Luis, *L. Anderson* 3077 (SI). **Santiago del Estero:** Guasayán, de Guampacha a Guasayán, *Rotman* 228 (SI). **Tucumán:** Trancas, ruta 9 al S de Choromoro, *Burkart* 30574 (SI).

- 17. *Aloysia peruviana*** (Turcz.) Moldenke, *Revista Sudamer. Bot.* 4: 15. 1937. Basionym: *Lippia peruviana* Turcz., *Bull. Soc. Imp. Naturalistes Moscou* 36(2): 200. 1863. TYPE: Peru. Puno-chuca, s.d., *W. Matthews* 585 (holotype, KW [barcode] KW001001633 not seen, KW image!; isotypes, BM [bc] BM000643629 not seen, BM image!, BR-562372 not seen, BR [bc] BR0000005623723 not seen, BR image!, K [bc] K000470998 not seen, K image!). Figure 9.

Aloysia aloysioides Loes. ex Moldenke, *Phytologia* 2: 9–10. 1941. *Lippia aloysioides* Loes. ex Moldenke, nom. inval. [cheironym]. *Phytologia* 2: 10. 1941. TYPE: Peru. Lima, below Surco, Feb. 1909, *A. Weberbauer* 5206 (holotype, F [barcode] F0043368 not seen, F image!; isotypes, NY [bc] NY00103865 not seen, NY image!, S11-10554 not seen, S image!, SI [bc] SI014007!, US [bc] US00118806 not seen, US image!).

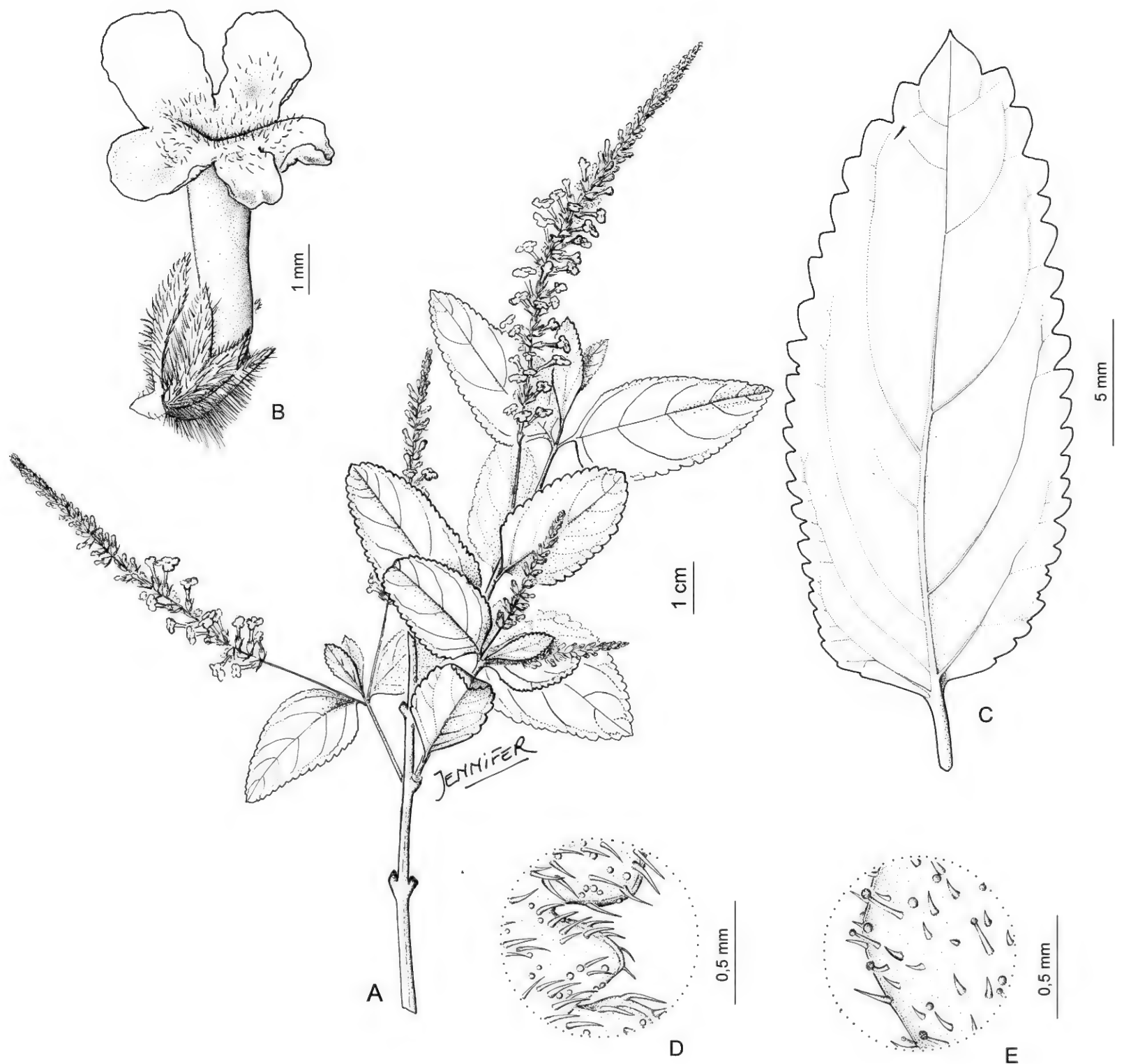


Figure 9. *Aloysia peruviana* (Turcz.) Moldenke. —A. Floriferous branch, with axillary florescences (homothetic pleiobotrya). —B. Intact flower in lateral view, with hispid calyx and subtending strigose floral bract (at left). —C. Intact leaf, abaxial surface, evenly crenate margin and prominent venation. —D. Close-up of abaxial leaf surface, with hispid indument. —E. Close-up of adaxial leaf surface with scattered strigose and hispid hairs. B, illustrated from *Soukup 4872* (US); A, C–E, taken from *Donovan P978* (US).

Aloysia minthiosa Moldenke, *Phytologia* 2: 12. 1941, syn. nov. TYPE: Peru. Ancash, Yaután, 9 Oct. 1922, *J. F. Macbride* 2564 (holotype, F [barcode] F0042838F not seen, F image!; isotypes, GH [bc] GH00299002 not seen, GH image!, NY [bc] NY00103882 not seen, NY image!, SI!).

Shrubs 1–2.5 m tall; stems lightly puberulent to strigose. Leaves generally opposite; petioles 0.2–0.5 cm long; blades ovate to elliptic, 2–4 × 1–2 cm, apex subobtusate, base rounded, margins evenly crenate, adaxially scabrous, abaxially hispid or strigose, venation pinnate and reticulate, conspicuous on abaxial surface, membranaceous and plane texture. Florescences axillary, solitary, dense, 8–10 cm;

peduncles 1–2 cm; flowers white or pale violet; pedicels 0.5 mm; floral bracts narrowly elliptic, 2–3 mm, apex acute, strigose. Flower with the calyx 2–2.5 mm, hispid, hairs longer proximally, grading to shorter distally, with 4 teeth, unequal, triangular; corolla tube 6–7(–8) mm, externally glabrous, with villous fauce. Cluses 2 × 1 mm, smooth and glabrous.

Distribution and habitat. *Aloysia peruviana* is endemic to Peru, growing at elevations from 1200 to 2000 m, on rocky slopes.

Discussion. *Lippia aloysioides* Loes. is an invalid name, only mentioned in the protologue of *Aloysia*

alloysioides where Moldenke (1941: 10) stated “The cheironym, *Lippia alloysioides* Loes., appears on the label.” A cheironym is an unpublished name and invalid.

Aloysia peruviana has perfumed, sweet-smelling flowers, with showy blooms and long corolla tubes 6–7(8) mm. There are also other species in *Aloysia* with long corollas. *Aloysia castellanosi* would be distinguished by its oblong leaf blades, these being ovate to elliptic in *A. peruviana*. *Aloysia crenata* and *A. citrodora* differ in their ternate leaves, these being opposite in *A. peruviana*. *Aloysia salsoloides*, *A. deserticola*, and *A. tarapacana* also may have long corollas, with lengths of 5–7 mm, 4–6 mm, and 5–6 mm, respectively. However, all three are plants with spiny branches and reduced leaf blades. Two varieties of *A. scorodonioides* also have long corollas, 5–6 cm in both *A. scorodonioides* var. *mathewsii* and *A. scorodonioides* var. *scorodonioides*. However, both varieties may be distinguished by rugose leaf textures, in contrast to a membranaceous texture in *A. peruviana*.

The type material of *Aloysia minthiosa*, described by Moldenke in 1941 from Peru, indicates its similarity to *A. peruviana*, with both sharing leaf and florescence morphology and also long corolla tubes. The name *A. minthiosa* is synonymized herein, to *A. peruviana*.

Siedo (2010) designated a superfluous lectotype for *Lippia peruviana* from BM, stating that all original material had been destroyed. This has proved inaccurate and the holotype has been confirmed to exist at KW in Kiev, where material studied by Turczaninow is housed (Natalia Shiyan, curator at KW, 2013, pers. comm.).

Selected specimens examined. PERU. **Ancash:** Km. 265 on rd. from Conococha to coast, *Donovan P978* (US). **Lima:** Km. 70 valle del Rimac, *Velarde Nuñez 301* (SI); Camino a Huarachiri, *Soukup 4872* (US); Surco, *Soukup 3741* (F); Santa Eulalia, 27 km from Chosica, *Gentry 44821* (MO); Santa Eulalia rd., N of Chosica, *Gentry 36089* (F); above Chosica, betw. Lima & Matucana, *Ferreyra 755* (NY, SI); Huarochiri, 7.5 km above Santa Eulalia rd., *Olmstead 2009-45* (SI, WTU); Canta, *Ferreyra 12952* (SI); Huarochiri, N Chosica, *Ferreyra 759* (F).

- 18. *Aloysia polygalifolia*** Cham., *Linnaea* 7: 236. 1832, as “polygalaefolia.” *Lippia polygalaefolia* (Cham.) Steud., *Nomencl. Bot.* [Steudel] 2(2): 54. 1841. TYPE: Brazil. s. loc., s.d., *F. Sellow s.n.* (lectotype, designated by Siedo [2010: 201], G [barcode] G00386462 not seen; isolectotype, E [bc] E00373271 not seen, E image!). Figure 10.

Shrubs 1–3.5 m tall. Leaves ternate, adpressed to stem; blades sessile, ovate to elliptic, $0.5\text{--}2 \times 0.3\text{--}1$

cm, apex acute, base truncate, margins entire, sometimes subrevolute, sclerophyllous, scabrous to strigose on both surfaces, sometimes glabrate, venation plane. Florescences axillary, solitary, dense, 4–13 cm; peduncles 1–3 cm. Flowers lilac; floral bracts sublinear, 2–3.5 mm, apex acuminate, strigose. Flower with the calyx 2–4 mm, hispid, 4-toothed, the teeth unequal, triangular; corolla tube 4–5 mm, externally finely pulverulent, internally with villous fauce. Cluses 1.5×1 mm, glabrous.

Distribution and habitat. *Aloysia polygalifolia* is endemic to Brazil from Paraná, Rio Grande do Sul, and Santa Catarina, and is found in disturbed and dry areas.

Discussion. *Aloysia polygalifolia* is similar to *A. cordata* because both have ternate leaves adpressed to the stem. Both have been collected from the state of Paraná, although *A. cordata* has been noted from more mesic conditions. However, *A. cordata* has cordate leaf blades that are glabrate and only minutely scaberulous, whereas leaf blades range from scabrous to strigose, with a truncate base, in *A. polygalifolia*. Exceptionally, leaves can be glabrate (Thode et al. 398, ICN) as in *A. cordata*, but the blades are never cordate in *A. polygalifolia*. *Aloysia polygalifolia* is also similar to *A. brasiliensis* (see discussion under *A. brasiliensis*).

Selected specimens examined. BRAZIL. **Paraná:** Palmas, Morro da Baliza, *Hatschbach 30734* (NY); Palmas, 10 km NO Palmas, *Hatschbach 28171* (NY). **Rio Grande do Sul:** Guaíba, faz. Sao Maximiano, BR-116, *Thode 398* (ICN, SI). **Santa Catarina:** Ponte Serrada, Fachinal dos Guedes, *Smith & Reitz 12478* (SI); Agua Doce, 5 km S of turn to rd. E to Palmas, *Smith 15683* (SI); Iraní, *Smith & Klein 13029* (SI); Agua Doce, campos de Palmas, *Smith & Klein 13577* (SI).

- 19. *Aloysia polystachya*** (Griseb.) Moldenke, *Lilloa* 5: 380. 1940. Basionym: *Lippia polystachya* Griseb., *Abh. Königl. Ges. Wiss. Göttingen* 19: 242. 1874. TYPE: Argentina. Córdoba: Las Mollas, Las Peñas, Jan. 1871, *P. G. Lorentz 130* (holotype, GOET [barcode] GOET008519 not seen, GOET image!; isotypes, [B†, B as F neg. 17535!], CORD [bc] CORD00006124 not seen, CORD image!, GOET [bc] GOET008520 not seen, GOET image!, K [bc] K000470937 not seen, K image!, US [bc] US01049797 not seen, US image!, SI [bc] SI004434!, SI [bc] SI003577!, VT [bc] UVMVT026110 not seen, VT image!).

Shrubs 0.5–1.5 m tall; stems glabrous at maturity, with short internodes. Leaves alternate, rarely

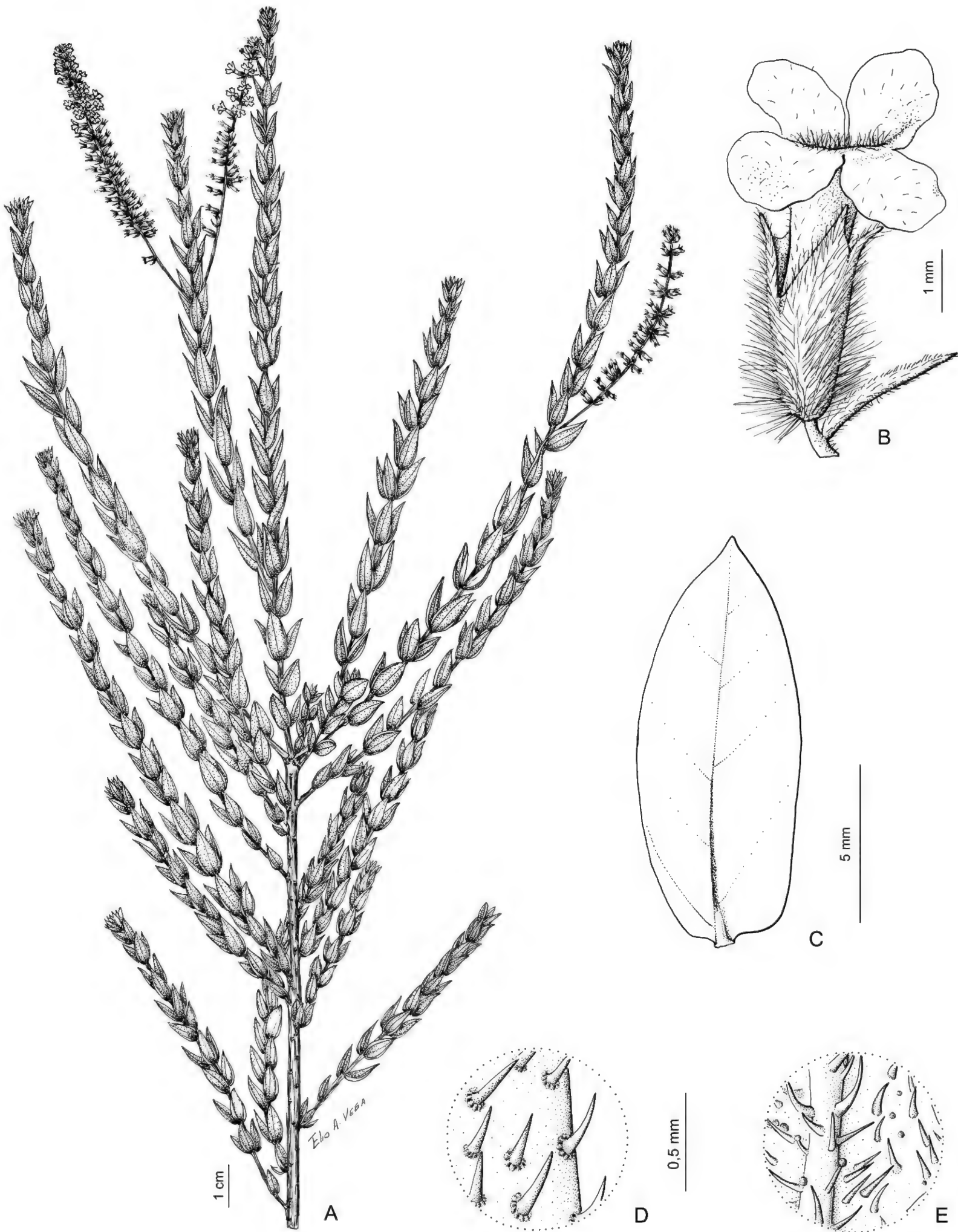


Figure 10. *Aloysia polygalifolia* Cham. —A. Floriferous branches, general aspect, with axillary floescences (homothetic pleiobotrya). —B. Intact flower with strigose floral bract subtending (at right) the hispid calyx. —C. Intact leaf, adaxial surface, venation plane. —D. Close-up of adaxial leaf surface, with strigose and scabrous indument. —E. Close-up of abaxial leaf surface, with strigose and scabrid indument. A, illustrated from *Smith & Klein 13577* (SI); B–E from *Smith & Klein 13029* (SI).

opposite, petioles 0.1–0.3 cm; blades elliptic, 1–5 × 0.3–1 cm, apex acute to subobtuse, base acute, attenuate, margin entire, adaxially scabrous, abaxially densely strigose. Florescences axillary, solitary or sometimes fasciculate, dense, short, 0.5–3 cm; peduncles 0.5–1 cm; flowers white, small; floral bracts reduced, obovate, 1–1.5 mm, hispid. Flowers with the calyx 1–1.5 mm, puberulous, with 4 teeth, brief, unequal, triangular; corolla tube 1.5–2 mm, externally puberulous, with villous fauce. Cluses 1 × 0.5 mm, glabrous.

Iconography. Botta (1979: 106, fig. 13).

Distribution and habitat. *Aloysia polystachya* has been observed to grow in central and northwestern Argentina, and Paraguay, on sandy soils.

Discussion. *Aloysia polystachya* is an aromatic plant, cultivated for medicinal properties (Arambarri et al., 2009). Siedo (2010) lectotypified this taxon, but this was superfluous, because the holotype has been confirmed to exist and is housed at GOET.

Aloysia polystachya is easily distinguished from other congeners since it has developed alternate leaves to 5 cm long. Only one other species, *A. salsoloides*, also has alternate leaves, but the leaf blades are reduced, always shorter than 0.5 cm.

Selected specimens examined. ARGENTINA. **Catamarca:** Belén, cult., *Arenas* 257 (SI). **Córdoba:** Punilla, Sierra Chica, Falda O, San Salvador, al N del Cerro Uritorco, Quebrada de Ochoa, *A. Hunziker* 8951 (SI). **Formosa:** Patiño, Las Lomitas, Barrio La Bomba, *Arenas* 3465 (SI). **La Rioja:** General San Martín, Ulapes, *Stuckert* 17046 (SI). **Salta:** Anta, *Luna* 147 (NY). **San Juan:** Valle Fertil, San Agustín, *Pedersen* 11796 (NY, SI). BOLIVIA. **Chuquisaca:** Azero, Estación Exp. zootécnica “El Salvador,” *Krapovickas* 31277 (SI). PARAGUAY. **Central:** Itá, *Arenas* 1916 (BACP). **Pte. Hayes:** Misión San Leonardo de Escalante, June 1981, *Sturzenegger s.n.* (BACP 2453).

20. *Aloysia pulchra* (Briq.) Moldenke, *Phytologia* 1: 95. 1934. Basionym: *Lippia pulchra* Briq., *Ark. Bot.* 2(10): 18. 1904. TYPE: Brazil. Rio Grande do Sul: Porto Alegre, 1892, *A. F. Regnell* 579 (holotype, G [barcode] G00386457 not seen, G image!; isotypes, F [bc] F0092929F not seen, F image!, G [bc] G00386456 not seen, G image!, NY [bc] NY00137807 not seen, NY image!, RB not seen, SI!, S11-10470 not seen, S image!, SI [bc] SI003403!, US [bc] US01049794 not seen, US image!).

Lippia sellowii Briq., *Annuaire Conserv. Jard. Bot. Genève* 4: 21. 1900, replacement name for *Lippia affinis* Briq., *Bull. Herb. Boissier* 4: 339. 1896, nom. illeg. superfl., non *Lippia affinis* Schauer ex DC., *Prod. [de Candolle]* 11: 576. *Aloysia uruguayensis* Moldenke, *Phytologia*

1(4): 167. 1935, nom. illeg. superfl. *Aloysia sellowii* (Briq.) Moldenke, *Revista Sudamer. Bot.* 4: 15. 1937. *Aloysia gratissima* var. *sellowii* (Briq.) Botta, *Darwiniana* 22: 85. 1979. TYPE: Uruguay. Montevideo, *F. Sellow* 1744 (holotype, G [barcode] G00386443 not seen, G image!; isotypes, [B†, B as F neg. 24670!], W not seen, W fragm. at SI 66318!).

Aloysia lycioides var. *revoluta* Moldenke, *Phytologia* 3: 108. 1949. *Aloysia gratissima* var. *revoluta* (Moldenke) Moldenke, *Phytologia* 9: 500. 1964. TYPE: Uruguay. s. loc., s. coll. [no label, probably collected by *J. Arachavaleta s.n.*] (holotype, MVM not seen; isotype, NY [barcode] NY00103880 not seen, NY image!).

Shrubs 1–3 m tall; stems glabrous. Leaves opposite, with brief petioles 2–8 mm; blades elliptic to obovate, 2–5 × 1–2 cm, apex obtuse, base acute, attenuate, margin entire, sometimes slightly serrate toward apex, coriaceous, adaxially scabrous, abaxially glabrate to slightly puberulous, venation pinnate, with lateral veins that converge in marginal vein. Florescences axillary, solitary, lax, 5–8 cm; peduncles 1–3 cm; flowers white; floral bracts ovate, apex acute, 1–1.5 mm, lightly strigose, margin ciliate. Flower with the calyx 2–3.5 mm, hispid in inferior half, lightly hispid toward apex, with 4 teeth, brief, unequal, triangular; corolla tube 4–5.5 mm, externally puberulous toward apex, with villous fauce. Cluses 1 × 0.5 mm, glabrous.

Iconography. Botta (1979: 80, fig. 4).

Distribution and habitat. *Aloysia pulchra* grows in the northeastern provinces of Argentina (Corrientes, Misiones), southern Brazil (Paraná, Rio Grande do Sul), Paraguay, and Uruguay.

Discussion. *Aloysia pulchra* differs from *A. gratissima* in its habitat preference, with the latter found in more xeric areas, and is a more xerophytic plant in appearance. Morphologically, *A. pulchra* has elliptic to obovate leaf blades, with entire margins and an obtuse apex. While leaves range from elliptic to ovate in *A. gratissima*, blade margins vary from entire to dentate or serrate, with acute or subobtuse apices. Both species are rather similar in general morphology, and subsequent studies are being performed in order to check the validity of these two taxa.

When published, the name *Lippia affinis* Briq. (Briquet, 1896) was superfluous and illegitimate because of the priority of *L. affinis* Schauer (1847), which affines with *Lippia* and not *Aloysia*. Briquet (1900) later realized this homonymy and created *L. sellowii* as a replacement name for the blocked *L. affinis* Briq. However, Moldenke (1935) did not realize Briquet had offered a replacement name and created another replacement name, also superfluous, as *A. uruguayensis* Moldenke.

Aloysia gratissima var. *sellowii* (Briq.) Botta is here considered a synonym of *A. pulchra* (Briq.) Moldenke, following Botta's (1979) observation about the close relationship between these two taxa.

Selected specimens examined. ARGENTINA. **Corrientes:** Capital, Riachuelo, *Martínez Crovetto* 10801 (SI). **Misiones:** Leandro Alem, Cerro Azul, *Cabrera* 28634 (SI); San Javier, Arroyo Lorenzo, *G. J. Schwarz* 3803 (NY). BRAZIL. **Paraná:** Palmeira, Papagaio, *Smith* 14930 (SI). **Rio Grande do Sul:** entre Chapada y Lajeado Grande, *Brescia & Marchesi* 4269 (SI). **Santa Catarina:** Isla do Francés, *Stienstra s.n.* (SI). PARAGUAY. **Alto Paraná:** in regione fluminis, *Fiebrig* 5904 (SI). **Paraguarí:** Cerro Mbatoví, *Zardini* 10036 (SI). URUGUAY. **Rivera:** bajada de Pena, *Del Puerto* 6053 (SI). **Tacuarembó:** Valle Edén, *Dematteis* 1531 (SI).

21. *Aloysia riojana* (Hieron. ex Moldenke) Lu-Irving & N. O'Leary, Syst. Bot. 39(2): 653. 2014. Basionym: *Acantholippia riojana* Hieron. ex Moldenke, Phytologia 3(3): 106. 1949. TYPE: Argentina. La Rioja, Vinchina, 5 Mar. 1879, *G. Hieronymus & G. Niederlein* 292 (lectotype, designated by Múlgura et al. [2012: 6], CORD [barcode] CORD00003809 not seen, CORD image!; isoelectotypes, CORD [bc] CORD00003810 not seen, CORD image!, G [bc] G00366265 not seen, G image!).

Shrubs 1–1.7 m tall; branches spiny, stems hispid to glabrate at maturity. Leaves small, opposite, adpressed to the stem, sessile, squamiform, imbricate; blades rhomboidal in outline, 1.5 × 1.5–2 mm, light green or yellow-green, 3-lobed with a large apical lobe and 1 lateral smaller lobe on either side, ± thickened texture, apex subobtusate, base rounded, margin entire, revolute, adaxially scabrous, abaxially with a conspicuous hirsute furrow on each blade lobe. Florescences terminal, solitary, dense, 12–15 mm; flowers lilac; floral bracts ovate or obovate, apex acute or obtuse, 3–3.5 mm, slightly strigose. Flowers with the calyx 3.5 mm, hispid, with 4 teeth, brief, unequal, triangular; corolla tube 4–6 mm, with villous fauce. Cluse 2–3 × 0.5 mm, orbicular in cross section, commissural faces connate.

Iconography. Botta (1980: 520, fig. 2).

Distribution and habitat. *Aloysia riojana* is endemic to Argentina (La Rioja, San Juan) where it is frequent on sandy soils along riversides. Collections have been made at elevations up to 1800 m.s.m.

Discussion. *Aloysia riojana* is similar to *A. deserticola*, both shrubs with spiny branches and small, sessile leaves that are squamiform, adpressed to stems with blades 3-lobed, with a conspicuous

furrow on each blade lobe. However, *A. riojana* differs from *A. deserticola* by its fruit with connate commissural cluses. Plants are taller and more graceful, to 1.7 m in *A. riojana* (vs. 1.5 m or less in *A. deserticola*) with more slender, less spiny, and longer branches.

Moldenke (1949: 106) mentioned a Berlin specimen identified in sched. as *Acantholippia riojana* by Hieronymus, who was one of the two collectors of the type. The Berlin sheet no longer exists and is the reason why Múlgura (2012: 6) lectotypified this name on a CORD specimen. Moldenke indicated in the protologue that Hieronymus never published the name, as in sched. and invalid, although Moldenke acknowledged Hieronymus as the source for the later validly published epithet, ascribing it as “Hieron. & Moldenke.” The two could not have collaborated on the epithet, given the difference in lifetimes (Hieronymus, 1846–1921; Moldenke, 1909–1996). The epithet is better attributed as Hieron. ex Moldenke (McNeill et al., 2012: Art. 46.5).

Selected specimens examined. ARGENTINA. **La Rioja:** Coronel Felipe Varela, cauce río Bermejo, c. Villa Unión, *Biurrun* 7705 (SI); Vinchina, en médano, *Hunziker* 2037 (SI). **San Juan:** Valle Fértil, ruta 510, cauce La Guardia, 2 km E de Baldecito, *Biurrun* 7696 (SI).

22. *Aloysia salsoloides* (Griseb.) Lu-Irving & N. O'Leary, Syst. Bot. 39(2): 653. 2014. Basionym: *Acantholippia salsoloides* Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 244. 1874. *Lippia salsoloides* (Griseb.) Briq., Nat. Pflanzenfam. [Engler & Prantl] 4(3a): 152. 1897. TYPE: Argentina. Catamarca: “ubi fruticeta praecipue constituit in planitie Laguna blanca, alt. 10000,” *P. G. Lorentz* 457 (holotype, GOET [barcode] GOET007269 not seen, GOET image!; isotypes, [B†, B as F neg. 17540!]; CORD [bc] CORD00006133 not seen, CORD image!, SI [bc] SI003359!).

Acantholippia hastulata Griseb., Symb. Fl. Argent., 279. 1879. *Lippia hastulata* (Griseb.) Hieron., Bol. Acad. Nac. Ci. 4: 407. 1882. TYPE: Argentina, *P. G. Lorentz & G. H. Hieronymus* 713 (holotype, CORD [barcode] CORD00006139 not seen, CORD image!; isotypes, [B†, B as F neg. 17511!]; GOET [bc] GOET008868 not seen, GOET image!, GOET [bc] GOET008867 not seen, GOET image!, SI [bc] SI003357!).

Shrubs 0.35–1.5 m tall; branches spiny; stems hispid, glabrate at maturity. Leaves alternate, adpressed to stem, sessile; blades reduced, ovate, 1.5–4.5 × 2 mm, 5-lobed with 1 large apical and 2 lateral small lobes on either side, ± thickened texture, apex subobtusate base rounded, margin entire, revolute, adaxially scabrous, abaxially hirsute, venation prom-

inent, reticulate. Florescences terminal, solitary, dense, 10–15 mm; flowers white; floral bracts ovate or obovate, apex acute or obtuse, 3–4 mm, slightly strigose. Flower with the calyx 3.5–4 mm, hispid, with 4 brief teeth, unequal, triangular; corolla tube 5–7 mm, with villous fauce. Cluse $2-3 \times 0.5$ mm, glabrous.

Iconography. Troncoso (1974: 347, fig. 12, k–n); Botta (1980: 524, fig. 4); Caro (1982: 9, fig. 1 and 13, fig. 2, sub *Aloysia hastulata*).

Distribution and habitat. *Aloysia salsoloides* grows in northwestern Argentina and southern Bolivia, noted as found in salty soils and at elevations to 3200 m.

Discussion. *Aloysia salsoloides* shares with *A. deserticola*, *A. riojana*, and *A. tarapacana* a shrubby habit with spiny branches and reduced leaf blades, with the leaves sessile and adpressed to stems. However, *A. salsoloides* is distinguished from these three by the alternate arrangement of its leaves that are 5-lobed and not squamiform nor imbricate. Leaves are opposite, squamiform, and densely imbricate, with blades either entire or 3-lobed in *A. deserticola*, *A. riojana*, and *A. tarapacana*.

Selected specimens examined. ARGENTINA. **Catamarca:** Belén, Laguna Blanca, *Cabrera* 32474 (SI). **Jujuy:** Humahuaca, *Zuloaga* 9170 (SI). **Salta:** Rosario de Lerma, 57 km pasando Pte. Integración Argentina-Chilena, *Cialdella* 407 (SI). BOLIVIA. **Potosí:** Uyuni, *Hicken* 17 (SI).

23. *Aloysia salviifolia* (Hook. & Arn.) Moldenke, Lilloa 5: 381. 1940. Basionym: *Verbena salviifolia* Hook. & Arn., Bot. Beechey Voy. 1: 42. 1830, as “*salviaefolia*.” *Lippia chilensis* Schauer, Prodr. [de Candolle] 11: 573. 1847, replacement name, non *Lippia salviifolia* Cham., Linnaea 7: 227. 1832. *Aloysia chilensis* (Schauer) Moldenke, Revista Sudamer. Bot. 4: 15. 1937. TYPE: Chile. “Hab. Coquimbo,” s.d., s. coll. (neotype, designated here, K [barcode] K000470996 not seen, K image!). Figure 11.

Shrubs 1–2 m tall; stems glabrous. Leaves opposite, rarely alternate, sessile, elliptic, 1–2(–4) \times 1(–1.5) cm, apex acute to subobtuse, base obtuse to subtruncate, margin basally entire, irregularly serrate toward apex or from mid-blade distally, abaxial and adaxial surfaces strigose, venation pinnate, reticulate, abaxially prominent. Florescences axillary, solitary, dense, 5–10 cm; peduncles 1–2 cm; flowers white; pedicels 0.5 mm; floral bracts widely ovate, large, 4–4.5 mm, apex acute, acuminate,

hispid. Flower with the calyx 2–3.5 mm, hispid, with underlayer of subsessile glandular trichomes, with 4 teeth, unequal, triangular; corolla tube 3–3.5 mm, externally and internally glabrous. Cluses 1.5×1 mm, glabrous.

Distribution and habitat. *Aloysia salviifolia* is found in Chile (Regions III, IV), and one collection exists from Argentina.

Discussion. *Aloysia salviifolia* is distinguished by its leaf blade base obtuse to subtruncate, and margin basally entire and irregularly serrate toward apex or from mid-blade distally, and venation pinnate, reticulate, and abaxially prominent. It is also differentiated by its large floral bracts, to 4–4.5 mm, surpassing the calyx, a feature not frequent in the rest of *Aloysia*.

Schauer (1847) considered that *Verbena salviifolia* Hook. & Arn. should be under *Lippia*, but the epithet’s use in *Lippia* was blocked by the prior name *L. salviifolia* Cham., so that Schauer proposed *L. chilensis* as the replacement name. When Moldenke (1940) later transferred *V. salviifolia* to *Aloysia*, the original epithet was not blocked by priority and was available for use within *Aloysia*.

Noltie (2010: 181) stated that no original material has been found from *Verbena salviifolia* at the E and K herbaria. Noltie mentioned that “Arnott’s MS description has been mistakenly attached to a sheet annotated ‘*Lippia chilensis* Schauer,’ bearing mixed specimens of *Lobb* 453 (K [barcode] K000470996) and a *Gillies s.n.* collection from Mendoza (K [barcode] K000470995), neither of which are not original material.” Consequently, a neotype is here selected, with the more representative *Lobb* 453 material from Chile here chosen.

Selected specimens examined. ARGENTINA. **Mendoza:** s. loc., *Gillies s.n.* (K). CHILE. s. loc., *Bridges* 1346 (SI). **Region III:** Atacama, San Felix, *Ricardi* 23967 (SI). **Region IV:** Coquimbo, Quebrada de Rivadavia, *Werdermann* 103 (SI); Paihuano, *Pfister* 8318 (SI).

24. *Aloysia scorodonioides* (Kunth) Cham., Linnaea 7: 234. 1832. Basionym: *Lippia scorodonioides* Kunth, Nov. Gen. Sp. [quarto ed.] 2: 269. 1818. TYPE: Ecuador. “in regno Quitensis,” s.d., *A. Bonpland* 2192 (holotype, P [barcode] P00307136 not seen, P image; isotype, SI [bc] SI003396!). Figure 12.

Shrubs 0.5–3(–4) m tall; stems canescent when young, puberulous to strigose on mature stems. Leaves opposite, petioles 0.5–1 cm, sometimes sessile; blades elliptic, ovate, or orbicular, 1–5(–7) \times 1–3(–4) cm, apex obtuse to subobtuse, base

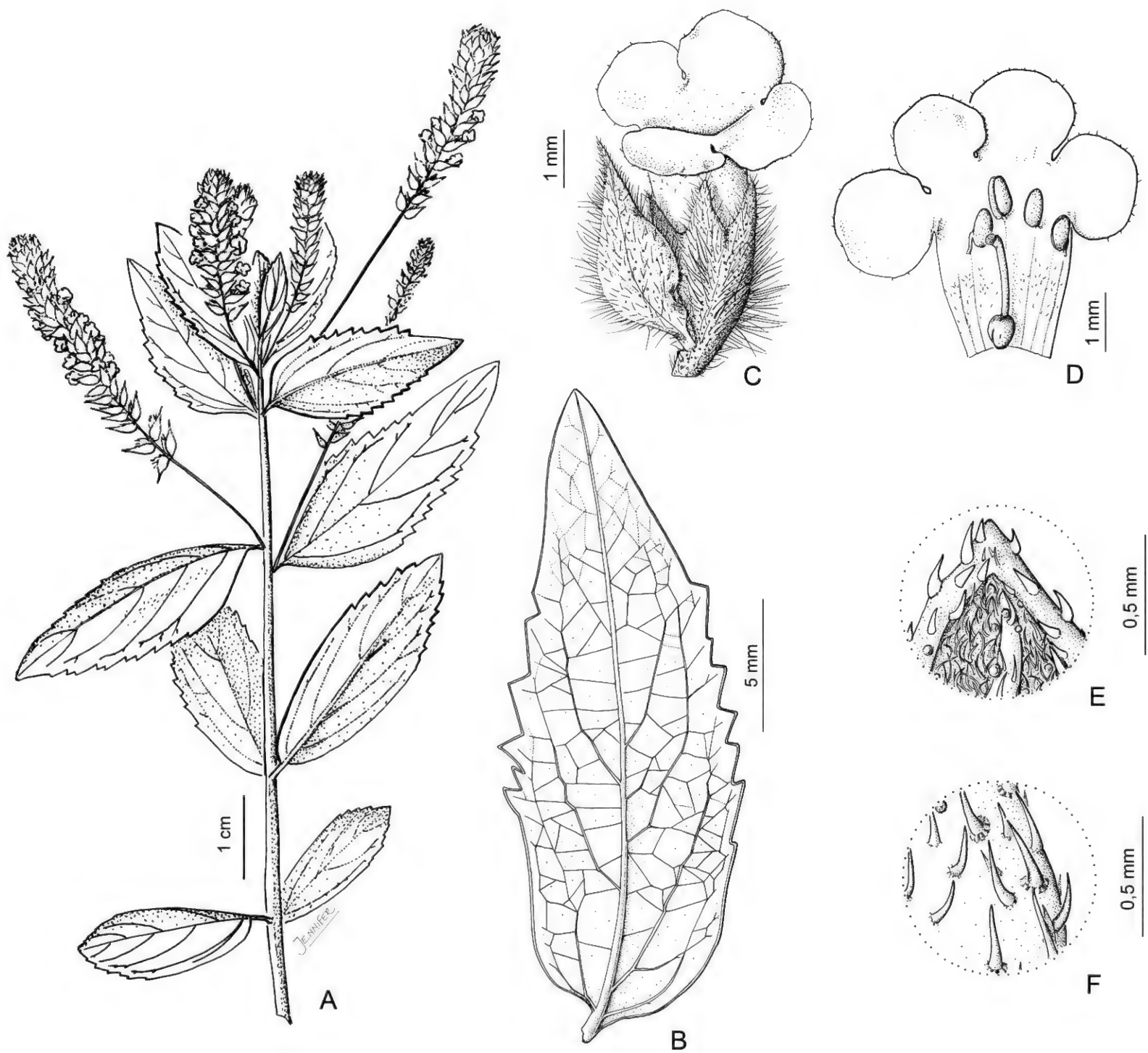


Figure 11. *Aloysia salviifolia* (Hook. & Arn.) Moldenke. —A. Floriferous branch with axillary florescences (homothetic pleiobotrya). —B. Entire leaf, abaxial surface, margin basally entire, irregularly serrate toward apex, prominent pinnate, reticulate venation. —C. Intact flower with hispid floral bract subtending, calyx hispid, with underlayer of subsessile glandular trichomes. —D. Corolla dissected open to reveal the androecium and gynoecium. —E. Close-up of abaxial leaf surface, with strigose and scabrid indument. —F. Close-up of adaxial leaf surface, with strigose indument. From *Bridges 1346* (SI).

acute, cordate, or rounded, margin evenly crenate, rugose and creased texture, sometimes membranaceous, adaxially scabrous, with conspicuous reticulate venation, abaxially hispid or tomentose. Florescences axillary, solitary, lax or dense, 1–9(–12) cm; peduncles 1–4 cm; flowers white, purple, or pink, small; floral bracts linear to narrowly ovate, subulate, 1–3 mm, strigose or scabrous. Flower with the calyx 2–3 mm, densely hispid, sometimes with long hairs in lower half, grading to shorter hairs toward apex, with 4 unequal teeth; corolla tube 4.5–6 mm, externally puberulous, with villous fauce;

ovary glabrous, sometimes slightly pilose. Cluses 2 × 1 mm, glabrate.

TAXONOMIC KEY TO THE VARIETIES OF *ALOYSIA SCORODONIOIDES*

1. Shrubs 0.5–2 m tall; leaves 1–2.5(–4) × 1–1.5(–2) cm, blades elliptic to ovate; florescences dense, 1–3(–4) cm long, straight; peduncles 1–3 cm long; corollas 4.5–5.5 mm long 24a. *A. scorodonioides* (Kunth) Cham. var. *hypoleuca* (Briq.) Moldenke
- 1'. Shrubs 2–3(–4) m tall; leaves 2–5(–7) × 2–3(–4), blades ovate to orbicular; florescences lax or dense, 4.5–12 cm long, curved, peduncles 2–4 cm long; corollas 5–6 mm long 2

2. Florescences lax, 8–12 cm long, peduncles 2–4 cm long 24b. *A. scorodonioides* (Kunth) Cham. var. *mathewsii* (Briq.) Moldenke
- 2'. Florescences dense, 4.5–8 cm long, peduncles 2 cm long 24c. *A. scorodonioides* var. *scorodonioides*

24a. *Aloysia scorodonioides* var. *hypoleuca* (Briq.) Moldenke, Phytologia 36(5): 437. 1977. Basionym: *Lippia scorodonioides* var. *hypoleuca* Briq., Bull. Herb. Boissier 4: 338. 1896. TYPE: Peru. s. loc., s.d., *J. Dombey* 259 (lectotype, designated by Siedo [2010: 203], G [barcode] 0386453 not seen, G image!, G as F neg. 24668!). Figure 12J–L.

Aloysia scorodonioides var. *parvifolia* Moldenke, Phytologia 36(5): 437. 1977. TYPE: Bolivia. Near La Paz, Oct. 1885, *H. H. Rusby* 920 (holotype, NY [barcode] NY00103890 not seen, NY image!; isotypes, BM [bc] BM000643654 not seen, BM image!, MO-116725 not seen, MO image!, NY [2, bc] 103888, 103889, not seen, NY images!, US [2, bc] 01013795, 1323004 not seen, US images!, WIS [bc] WIS0256108 not seen, WIS image!).

Aloysia depressa Ravenna, Onira 11(4): 15. 2007, syn. nov. TYPE: Bolivia. La Paz, Feb.–Mar. 1933, *M. Doello-Jurado* s.n. (holotype, BA-9827!).

Aloysia axillaris J. R. I. Wood, Kew Bull. 64: 521. 2009, syn. nov. TYPE: Bolivia. Potosí, Torotoro, Cañon del Vergel, 2591 m, 3 Jan. 2000, *J. R. I. Wood*, *M. Mercado* & *T. Ortuño* 21305 (holotype, K [2, barcode] K000738254 not seen, K image!, K [barcode] K000738253 not seen, K image!; isotypes, BOLV not seen, LPB [bc] LPB0000838 not seen, LPB image!).

Shrubs 0.5–2 m tall; stems puberulous. Leaves 1–2.5(–4) × 1–1.5(–2) cm; blades elliptic or ovate. Florescences dense, 1–3(–4) cm, straight; peduncles 1–3 cm. Flowers pink to purple, corolla tubes 4.5–5.5 mm.

Distribution and habitat. *Aloysia scorodonioides* var. *hypoleuca* has a narrow distribution being found only in Peru and Bolivia growing on open, dry hillsides in loose gravel and shallow soils, at elevations to 3070 m.

Discussion. In Cuzco, Peru, near Calca, there are some specimens with lax florescences with flowers spaced apart 3 mm, e.g., *Olmstead* 2009-40 (WTU), *Vargas* 160 (SI), and *Cook* 247 (US).

In his 2009 protologue, Wood stated that *Aloysia axillaris* was distinguished by two different inflorescence forms, one with solitary axillary flowers without floral bracts and the second with axillary spikes typical for the genus. These plants were observed to be restricted to two areas in Bolivia, from Potosí and Cochabamba. The author

noted the possibility of a hybrid origin for *A. axillaris*. The analysis of the type material and the description of the plant indicate that this corresponds to *A. scorodonioides* var. *hypoleuca*, with both sharing small leaf blades, shorter than 4 cm, with elliptic to ovate shapes. *Aloysia axillaris* differs principally in the presence of solitary flowers that lack floral bracts; this may be a localized somatic mutation in two known populations in Bolivia, which is here interpreted as of teratological or hybrid origin.

The study of the type material of *Aloysia depressa* Ravenna indicates that this is the same as *A. scorodonioides* var. *hypoleuca*. Both have the distinctive leaves of this variety (small elliptic to ovate blades) and dense florescences shorter than 4 cm.

Selected specimens examined. BOLIVIA. **Cochabamba:** Quillacolo, La Cabaña, *Wood* 20173 (BOLV, K, LPB). **La Paz:** Murillo, Mecapaca, *Beck* 3530 (SI). PERU. **Cajamarca:** Obrajillo, 1838–1842, *Wilkes* s.n. (US). **Cuzco:** Calca, 2 km from Pisac, *Olmstead* 2009-40 (WTU). **Huancavelica:** Tayacaja, entre Izcuchaca y Acostambo, *Hutchison* 4201 (US). **Lima:** Huarochirí, c. Matucana, *Ferreyra* 7021 (SI); Matucana, *Macbride* 133 (US); Km. 86, Lima–Oraya, *Ferreyra* 7013 (NY, SI).

24b. *Aloysia scorodonioides* var. *mathewsii* (Briq.) Moldenke, Phytologia 1: 95. 1934. Basionym: *Lippia scorodonioides* var. *mathewsii* Briq., Bull. Herb. Boissier 4: 339. 1896. TYPE: Peru. s. loc., *W. Mathews* 3160 (holotype, G [barcode] G00386446 not seen, G image! as F neg. 24669!; isotypes, G [bc] G0386464 not seen, G image!, K [bc] K000545990 not seen, K image!). Figure 12M.

Aloysia scorodonioides var. *lopez-palacii* Moldenke, Phytologia 36(5): 437. 1977. TYPE: Ecuador. Pichincha: Quito, 4 Feb. 1977, *S. López-Palacios* 4249 (holotype, TEX-LL [barcode] LL00374940 not seen, TEX-LL image!).

Shrubs 2–3(–4) m tall, stems canescent when young, strigose at maturity. Leaves 2–5(–7) × 2–3(–4) cm, blades ovate to orbicular, with rugose texture. Florescences lax, long, flowers not densely disposed, 8–12 cm, curved; peduncles 2–4 cm. Flowers white or pink, with corolla tubes 5–6 cm.

Distribution and habitat. *Aloysia scorodonioides* var. *mathewsii* grows in Ecuador, Peru, Bolivia, and northern Argentina. This variety has been collected from elevations of 900–2600 m.

Discussion. *Aloysia scorodonioides* var. *mathewsii* is distinguished by its long florescences, 8–12 cm, with flowers laxly disposed. This contrasts with the dense florescences 4.5–8 cm long in the autonymic variety,

and the shorter florescences less than 4 cm in *A. scorodonioides* var. *hypoleuca*.

Selected specimens examined. ARGENTINA. **Chaco:** Quitilipi, borde bosque, *Schulz* 2985 (SI). **Jujuy:** Santa Barbara, ruta Prov. 6, de Santa Clara a Abra de los Morteros, 12 km de Santa Clara, *Zuloaga* 11490 (SI). **Salta:** Anta, San Javier, *Saravia Toledo* 1764 (SI). BOLIVIA. **Chuquisaca:** Luis Calvo, Boyuibe, *Beck* 9428 (SI). ECUADOR. **Pichincha:** Tumbaco, *Asplund* 6533 (US). PERU. **Ápurímac:** Abarcay, *Vargas* 594 (SI). **Cajamarca:** Jaén, Km. 127, rd. Bagua to Pucara, *Lu-Irving* 9-62 (SI, WTU); Pucará, 127 km E Olmos, *Hutchison* 3520 (US). **Cuzco:** Calca, *Cook* 247 (US).

24c. *Aloysia scorodonioides* (Kunth) Cham. var. *scorodonioides*. Figure 12A–I.

Lippia scorodonioides var. *detonsa* Briq., Bull. Herb. Boissier 4: 339. 1896. *Aloysia scorodonioides* var. *detonsa* (Briq.) Moldenke, Phytologia 1: 95. 1934. TYPE: Colombia. “In montibus Columbiae,” s.d., *K. T. Hartweg* 1349 (holotype, BR [barcode] BR000000550590 not seen, BR image!; isotype, OXF not seen).

Aloysia leptophylla Loes ex Moldenke, Phytologia 2: 11. 1941, syn. nov. TYPE: Peru. s. loc., 1909–1914, *A. Weberbauer* 5374 (holotype, F [barcode] V0042839F! not seen, F image!; isotypes, NY [bc] NY00103878 not seen, NY image!, SI!).

Aloysia scorodonioides var. *orbicularis* Moldenke, Phytologia 3: 406. 1951. TYPE: Colombia. Yuaco, near Pasto, Nariño, s.d., *G. K. Wilhelm Hermann Karsten* s.n. (holotype, W [barcode] W0032435 not seen, W image!).

Aloysia boliviensis Moldenke, Phytologia 53(7): 460. 1983. TYPE: Bolivia. La Paz, Murillo, Mecapaca, 28 Mar. 1982, *J. C. Solomon* 7410 (holotype, TEX-LL [barcode] LL00374935 not seen, TEX-LL image!; isotypes, LPB [bc] LPB0000841 not seen, LPB image!, MO-3006114 not seen, MO image!, SI [bc] SI003375!, U [bc] U0006999 not seen, U image!).

Shrubs 2–3(–4) m tall, stems canescent when young, strigose at maturity. Leaves 2–5(–7) × 2–3(–4) cm, blades ovate to orbicular, rugose texture. Florescences dense, 4.5–8 cm, curved; peduncles 2 cm long. Flowers white or pink, corolla tubes 5–6 cm.

Distribution and habitat. *Aloysia scorodonioides* var. *scorodonioides* is found in Colombia, Ecuador, Peru, Bolivia, Paraguay, and northern Argentina. It has been collected from dry, brushy slopes, from open xeric, calcareous soils, and at elevations of 800–2800 m. Flowers are said to be very fragrant.

Discussion. The study of the type material of *Aloysia leptophylla* shows that this species corresponds to *A. scorodonioides* var. *scorodonioides*, sharing dense florescences 4.5–8 cm long.

There has been confusion about the attribution of the author of *Aloysia leptophylla*, since the holotype

sheet from F has a label, by Moldenke, that reads: “*Aloysia leptophylla* Loes.” In the protologue, Moldenke (1941: 11) attributed the name as “Loes. & Moldenke.” Given the differences in life spans (Loesener, 1865–1941; Moldenke, 1909–1996), it is unlikely Moldenke collaborated with Loesener, but rather credited Loesener for the unpublished name (nom. ined.). There is no further mention of Loesener by Moldenke and the ascription of the plant name should be Loes. ex Moldenke (McNeill et al., 2012: Art. 46.5).

Selected specimens examined. ARGENTINA. **Jujuy:** El Carmen, Pampa Blanca, *Cabrera* 29961 (SI). **Salta:** Anta, sector II, *Saravia Toledo* 1591 (SI). **Tucumán:** Burruyacu, Cañada Alegre, *Stuckert* 21287 (SI); s. loc., *Venturi* 849 (SI). BOLIVIA. **La Paz:** Loayasa, *Beck* 6039 (SI); Illimani, Nov. 1911, *Buchtien* 3240 (NY, SI). **Santa Cruz:** Cordillera, Charagua, *Cabrera* 33665 (SI). ECUADOR. **Esmeraldas:** Lita–San Lorenzo rd., *Gentry* 70190 (MO). **Loja:** near Saraguro, *Hart* 1481 (US). **Pichincha:** Guailabamba valley at Quito, *Haught* 3155 (US). **Tungurahua:** Ambato, *Pachano* 120 (US). PARAGUAY. s. loc., 1896, *Drake* s.n. (SI). PERU. **Cajamarca:** Celendin, valley rio Marañon, *Lu-Irving* 9-32 (SI, WTU). **Cuzco:** Anta, *Vargas* 3692 (SI). **Lima:** along rio Chillón, *Pennell* 14438 (US).

25. *Aloysia tarapacana* (Botta) Lu-Irving & N. O'Leary. Syst. Bot. 39(2): 653. 2014. Basionym: *Acantholippia tarapacana* Botta, Hickenia 1(35): 197. 1979. TYPE: Chile. Tarapacá, Arica, Puquios, 3750 m.s.m., 16 Sep. 1955, *M. Ricardi* 3363 (holotype, SI [barcode] SI003356!; isotypes, CONC not seen, LP [bc] LP006687 not seen, LP image!).

Shrubs 0.5–1 m tall, stems cylindrical, with spiny branches, hispid when young, glabrate at maturity. Leaves opposite, adpressed to the stem, sessile, squamiform, imbricate; blades reduced, rhomboidal, 2 × 1 mm, dark green, texture ± thickened, apex subobtuse, base rounded, margin entire, revolute, adaxially scabrous, abaxially hirsute. Florescences terminal, solitary, dense, 6–12 mm; flowers blue; floral bracts ovate or elliptic, apex acute or obtuse, 4.5 mm, slightly strigose. Flower with the calyx 4 mm, hispid, with 4 brief teeth, unequal, triangular; corolla tube 5–6 mm, with villous fauce. Cluse 2 × 0.5 mm.

Iconography. Botta (1980: 522, fig. 3).

Distribution and habitat. *Aloysia tarapacana* is endemic to Chile (Region I), collected at elevations from 3000 to 3390 m.

Discussion. *Aloysia tarapacana* is similar to *A. deserticola* and *A. riojana*, with a shrubby habit and

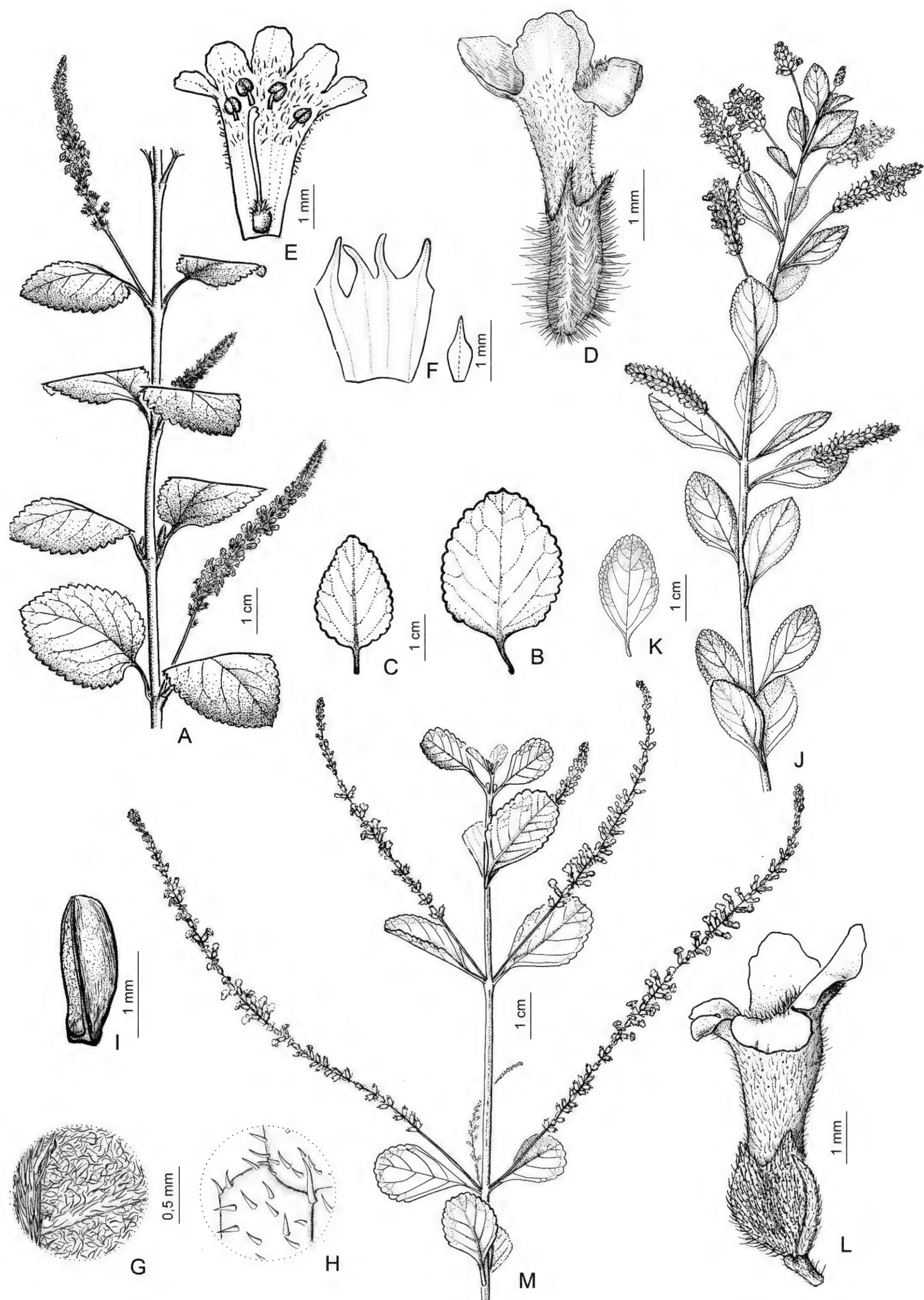


Figure 12. *Aloysia scorodonioides* (Kunth) Cham. A–I. *Aloysia scorodonioides* var. *scorodonioides*. —A. Floriferous branch with axillary florescences (homothetic pleiobotrya). —B. Basal leaf, orbicular blade. —C. Apical leaf, ovate blade. —D. Intact flower with hispid calyx. —E. Corolla dissected open to reveal the androecium and gynoecium. —F. Dissected calyx and floral bract, scheme. —G. Close-up of abaxial leaf surface, with hispid indument. —H. Close-up of adaxial leaf surface, with scabrid indument. —I. Cluse, lateral view. J–L. *Aloysia scorodonioides* var. *hypoleuca* (Briq.) Moldenke. —J. Floriferous branch with

spiny branches. In all three species, the leaf blades are in opposite position, reduced and squamiform, and densely imbricate along the stems. *Aloysia tarapacana* may be distinguished by its leaf blades with entire margins and dark green in color. Leaves are 3-lobed, with a conspicuous furrow on each blade lobe, and light green or yellow in color in both *A. deserticola* and *A. riojana*.

Selected specimens examined. CHILE. **Region I:** Arica, Antes de Zapahuina, *H. Escobar* 233 (SI); Parinacota entre Zapahuira y Putre, *Cocucci et al.* 3277 (SI).

26. *Aloysia trifida* (Gay) Lu-Irving & N. O'Leary. Syst. Bot. 39(2): 653. 2014. Basionym: *Lippia trifida* Gay, Fl. Chil. 5: 29. 1849. *Acantholippia trifida* (Gay) Moldenke, Lilloa 5(2): 371. 1940. TYPE: Chile. Copiapó, Feb. 1843, *C. Gay* s.n. (holotype, G [barcode] G00366065 not seen, G image!).

Lippia fonckii Phil., Anales Univ. Chile 90: 620. 1895, syn. nov. *Aloysia fonckii* (Phil.) Moldenke, Phytologia 2: 50. 1941. TYPE: Chile. Coquimbo, "prope La Higuera in litorali prov. Coquimbo," s.d., *F. S. Fonck* s.n. (holotype, SGO not seen, SGO image!; isotypes, SGO not seen, image!, SI [barcode] SI003514!).

Aloysia reichei Moldenke, Lilloa 5: 380. 1940, as "reichii," syn. nov. TYPE: Chile. Huanta, cordillera de Coquimbo, Jan. 1904, *K. F. Reiche* 19 (holotype, SGO-4203 not seen, SGO-4203 image!; isotype, SI [barcode] SI003393!).

Aloysia reichei var. *trilobata* Moldenke, Phytologia 2: 309. 1947. TYPE: Chile. Coquimbo, Elqui, Rio Turbio, 19 Oct. 1940, *R. Wagenknecht* 4238 (holotype, NY [barcode] NY103886 not seen, NY image!; isotypes, SGO-4204 not seen, SGO-image!, SI [bc] SI003408!).

Shrubs 1–2 m tall; stems cylindrical, hispid when young, glabrate at maturity. Leaves opposite, sessile, blade entire, ovate to elliptic, or 3-parted, 3.5–4.5 × 2–3.5 mm, somewhat thickened texture, apex acute to obtuse, base attenuate, margin entire, scabrous on both surfaces. Florescences axillary, solitary, dense, 1.5–3 cm; flowers white; floral bracts ovate, apex acute or obtuse, 3–3.5 mm, slightly strigose. Flowers with the calyx 2–2.5 mm, hispid, with 4 teeth, brief, unequal, triangular; corolla tube 4–5 mm, with villous fauce; superior pair of stamens with glandular appendices to anther connectives. Cluse 2–3 × 0.5 mm.

Iconography. Botta (1980: 518, fig. 6); Caro (1982: 27, fig. 5).

Distribution and habitat. *Aloysia trifida* is known from Chile (Regions III and IV) and also grows in Argentina (La Rioja, San Juan). Carmona and Ancíbor (1995) established that leaf anatomical characters indicated that this species was probably a facultative halophyte. This species has been collected from elevations up to 2500 m.

Discussion. *Aloysia trifida* is the only taxon in *Aloysia* known to have glandular appendices on the anther connectives of the superior pair of stamens. This species is also distinguished by its leaf blades entire, ovate to elliptic, but sometimes 3-parted.

The type material examined for *Aloysia reichei* has 3-parted leaves, as well as the distinctive glandular appendices on the anther connectives of the upper stamen pair. These are both characters exclusively observed in *A. trifida* and why *A. reichei* is synonymized to the species. The type specimen of *Lippia fonckii* also shares these characters, and this species name is also synonymized to *A. trifida*.

Selected specimens examined. ARGENTINA. **La Rioja:** Coronel Felipe Varela, ruta 40, entre Villa Unión y Sañogasta, 5 km E Puerto Alegre, *Biurrun et al.* 7706 (SI). **San Juan:** Calingasta, camp. Castaño, *Kiesling et al.* 9130 (SI). CHILE. **Region III:** Atacama, Copiapó, ruta a San Francisco, 61 km E interseccion ruta Paipote y Inca de Oro, *Taylor & Pool* 11607 (MO, SI). **Region IV:** Coquimbo, La Laguna, *Jiles* 5079 (SI).

27. *Aloysia velutina* Siedo, Lundellia 15: 44, fig. 4. 2012. TYPE. Peru. Cajamarca: Mpio. Cajamarca, sobre el km 156 de la carr. Pacasmayo–Cajamarca, bosque espinoso, 2000 m, 5 Apr. 1982, *I. Sanchez Vega* 2763 (holotype, F [barcode] F0093715F not seen, F image!; isotypes, MO not seen, SI [bc] SI080019!). Figure 13.

Shrubs 1–1.5 m tall; stems glabrous. Leaves opposite, with an occasional third leaf per node and ternate, petioles 0.3–1 cm long; blades ovate to elliptic, 3–6 × 1–5 cm, apex acute to subobtuse, base rounded to truncate, margin slightly crenate along entire blade, adaxially velutinous, abaxially incanous. Florescences terminal and axillary, dense, 8–15(–25) cm; peduncles 1–3 cm; flowers violet or cream-white, sometimes with lavender tubes and white lobes; pedicels 0.5 mm; floral bracts ovate,

←
axillary florescences (homothetic pleiobotrya). —K. Leaf, elliptic blade. —L. Intact flower with strigose floral bract subtending. M. *Aloysia scorodonioides* var. *matthewsii* (Briq.) Moldenke. —M. Floriferous branch with axillary florescences (homothetic pleiobotrya). A–F, I are illustrated from *Venturi* 849 (SI); G, H, from *Haught* 3155 (US); J–L, from *Macbride* 133 (US); M, from *Saravia Toledo* 1764 (SI).

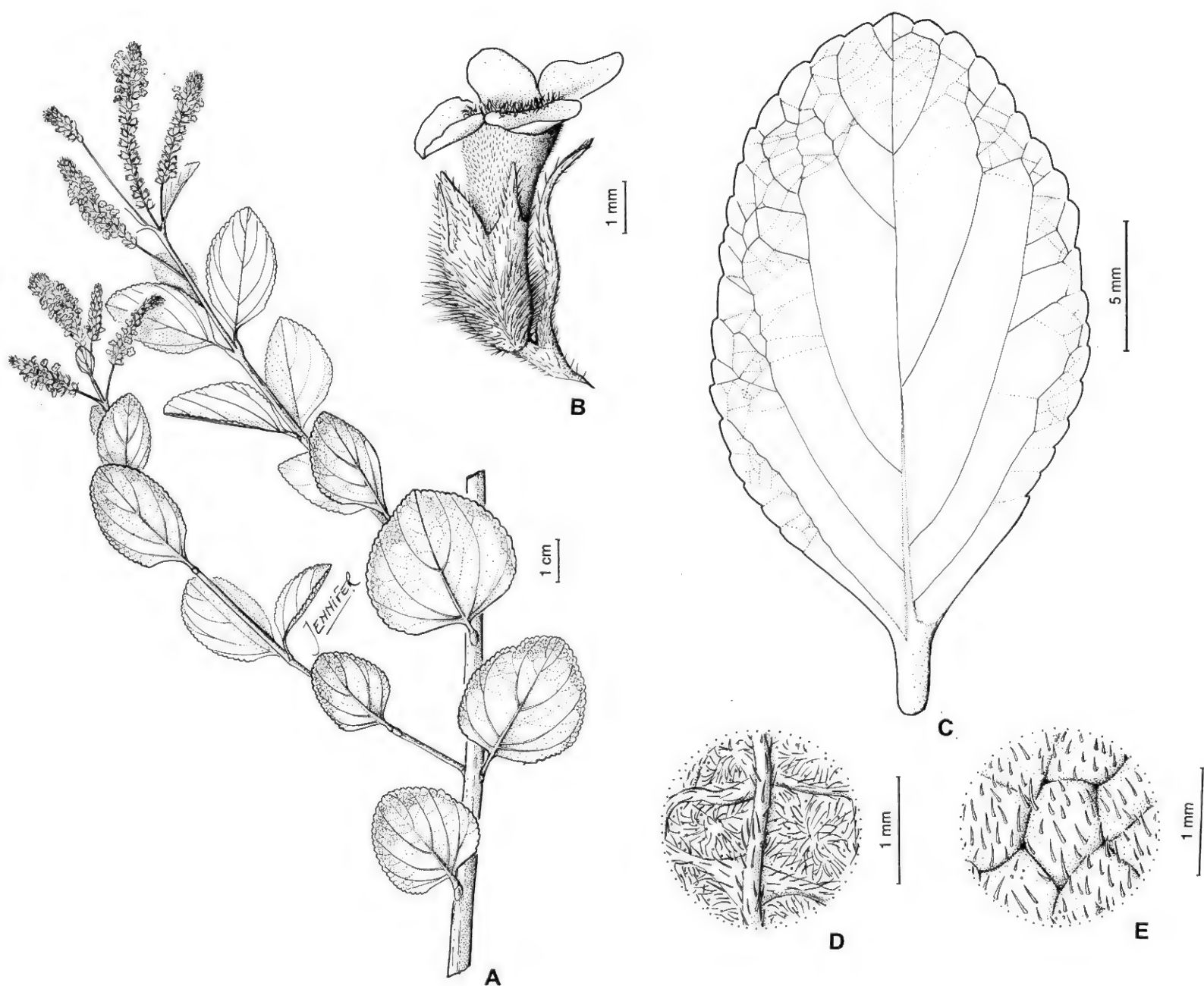


Figure 13. *Aloysia velutina* Siedo. —A. Floriferous branch, with both axillary and terminal florescences (heterothetic pleiobotrya). —B. Flower with hispid calyx and floral bract. —C. Leaf adaxial surface. —D. Close-up of abaxial leaf surface, with incanous indument. —E. Close-up of adaxial leaf surface, with scabrid indument. A, B from Sagástegui 14147 (SI); C–E from Llatas Quiroz 1953 (SI).

small, 2–2.5 mm, apex acute, acuminate, strigose, or hispid. Flower with the calyx 2–2.5 mm, hispid, with 4 teeth, unequal, triangular; corolla tube 3–3.5 mm, externally puberulous, with villous fauce. Cluses 1.5×1 mm, glabrous.

Distribution and habitat. *Aloysia velutina* is endemic and known only from woodland habitats in Cajamarca, Peru.

Discussion. *Aloysia velutina* has violet or cream-white flowers, sometimes with lavender tubes and white lobes, and sometimes three leaves per node (e.g., Olmstead 2009-8, WTU). The species is quite similar in leaf and florescence appearance to *A. scorodonoides* var. *scorodonoides*. However, *A. velutina* has both axillary and terminal florescences, whereas florescences appear only axillary in *A. scorodonoides*, even if this trait is not always easy to observe. The inflorescence morphology in *A.*

velutina (presence of both terminal and axillary florescences) groups *A. velutina* with *A. arequipensis*, *A. citrodora*, *A. fiebrigii*, and *A. herrerae*. However, *A. velutina* is easily distinguished by its opposite leaves that are ovate to elliptic, which contrasts with the ternate leaves of *A. citrodora* and the verticillate leaves, in whorls of three, with narrower blades (linear to elliptic) for *A. fiebrigii*. The shallowly crenate margins of the leaves of *A. velutina* easily distinguish this species from *A. herrerae* and *A. arequipensis*. Leaves seem longer in *A. velutina* too ($3\text{--}6 \times 1\text{--}5$ cm) versus $1\text{--}2 \times 0.5\text{--}1.2$ cm in *A. arequipensis* and $2\text{--}5.5 \times 0.4\text{--}1.5$ cm in *A. herrerae*. Leaf margins are entire in the former, and margins are finely serrate in the apical two thirds to one half of the blade in the latter.

Selected specimens examined. PERU. **Cajamarca:** Contumazá, ca. 2 km from Contumazá, Dillon 4544 (SI). **Cuzco:** Anta, Canyon rio Apurimac, 0.5 km from Pte. Cunyac,

Olmstead 2009-8 (WTU). **La Libertad:** Otuzco, alrededor San Ignacio, *Sagástegui 14147* (SI). **Lambayeque:** Ferre-afe, Incahuasi, *Llatas Quiroz 1953* (SI).

28. *Aloysia virgata* (Ruiz & Pav.) Pers., Syn. Pl. 2(1): 139. 1806. Basionym: *Verbena virgata* Ruiz & Pav., Fl. Peruv. 1: 20. 1798. *Aloysia virgata* (Ruiz & Pav.) Juss., Ann. Mus. Natl. Hist. Nat. 7: 73. 1806, nom. inval. *Zappania virgata* (Ruiz & Pav.) Poir., Encycl. [J. Lamarck et al.] 8: 845. 1808, as “*Zapania virgata*.” *Priva virgata* (Ruiz & Pav.) Spreng., Syst. Veg. [Sprengel] 2: 753. 1825. TYPE: [Peru. Pasco:] “Pozuzo,” 1827, *J. A. Pavón s.n.* [Herb. Pavón 36] (holotype, P [barcode] P000713759 not seen, P image; isotypes, G [bc] G00236936 not seen, G image!, G [bc] G00236923 not seen, G image, G [bc] G00386451 not seen, G image!, G [bc] G00386450 not seen, G image!, MPU [bc] MPU011501 not seen, MPU image!, P [bc] P000713760 not seen, P image!, SI [P fragm., photo!]).

Shrubs 2–7 m tall, stems hirsute, glabrate at maturity. Leaves opposite; petioles 3–10 mm; blades elliptic to ovate, 4–9(–15) × 1.5–4 cm, apex acute to subobtusate, base acute, subobtusate, or truncate, margin evenly minutely serrate or crenate, sometimes almost entire in appearance, membranaceous to coriaceous, adaxially strigose, abaxially hirsute, with prominent venation. Florescences axillary, solitary or 2 to 5, sometimes 7, per leaf axil, lax, subpendulous, 10–20 cm; peduncles 1–3 cm, sometimes branched; flowers white or cream, small; floral bracts linear to narrowly elliptic, 2–3 mm, hirsute. Flower with the calyx 2.5–3.5 mm, densely hispid, with long hairs and subsessile glandular trichomes, with 4 teeth, unequal, acute, subulate, the teeth equaling or exceeding the calyx tube in length; corolla tube 2.3–3.5 mm, externally puberulous toward apex, with villous fauce. Cluses 1 × 0.5 mm, glabrate.

Iconography. Botta (1979: 97, fig. 9).

Discussion. Leaves of *Aloysia virgata* are said to be used for therapeutical matters, such as antifungal treatments (Arambarri et al., 2008, 2009).

Aloysia virgata (Ruiz & Pav.) Juss. is an invalid combination (McNeill et al., 2012: Art. 33.1); Jussieu assigned *Verbena virgata* Ruiz & Pav. to *Aloysia*, but did not make the formal combination.

TAXONOMIC KEY TO THE VARIETIES OF *ALOYSIA VIRGATA*

1. Leaf apex acute, blades with acute to subobtusate base, high blade length/width ratios; ovary glabrous 28b. *A. virgata* (Ruiz & Pav.) Juss. var. *virgata*

- 1'. Leaf apex subobtusate, blades with obtuse to truncate base, low blade length/width ratios; ovary pilose 28a. *A. virgata* (Ruiz & Pav.) Juss. var. *platyphylla* (Briq.) Moldenke

28a. *Aloysia virgata* (Ruiz & Pav.) Pers. var. **platyphylla** (Briq.) Moldenke, Phytologia 2: 408. 1948. Basionym: *Lippia virgata* var. *platyphylla* Briq., Annuaire Conserv. Jard. Bot. Genève 7–8: 304. 1904. TYPE: Paraguay. Paraguarí, Mar. 1881–1884, *B. Balansa 3116* (lectotype, designated by Siedo [2010: 203], F-876782!; isoelectotypes, BM [barcode] BM000098764 not seen, BM image!, G [bc] G00166263 not seen, G image!, GH [bc] GH00312629 not seen GH image!, K [bc] K000471000 not seen, K image!, K [bc] K000487001 not seen, K image!, P [bc] P02851828 not seen, P image!, SI [bc] SI003609!).

Lippia virgata var. *elliptica* Briq., Annuaire Conserv. Jard. Bot. Genève 7–8: 304. 1904. *Aloysia virgata* var. *elliptica* (Briq.) Moldenke, Phytologia 1: 441. 1940. TYPE: Paraguay. L'Assomption, 15 abr. 1874, *B. Balansa 1016* p.p. (holotype, G [barcode] G00166264 not seen, G image!; isotypes, G [bc] G00381090 not seen, G image!, G [bc] G00381089 not seen, G image!, BR [bc] BR0000005505258 not seen, BR image!, P [bc] P02851832 not seen, P image!, SI!, SI1-10533 not seen, S image!).

Aloysia naviculata Ravenna, Onira 11(4): 16–17. 2007. TYPE: Paraguay. Dpto. Cordillera: Colonia Ojopoí E de Piribebuy, 3 June 1985, *P. Arenas 2912* (holotype, BA-90077!).

Shrubs with ovate leaf blades, almost the same length as width, with subobtusate apex, and obtuse to truncate base. Pilose ovary.

Distribution and habitat. *Aloysia virgata* var. *platyphylla* grows in Bolivia, Paraguay, and Argentina. In this last country, this variety exhibits a wider distribution than the type variety. *Aloysia virgata* var. *platyphylla* has been collected from woods and thickets on dry or wet ground, in forest patches or xerophytic areas.

Discussion. In the new combination *Aloysia virgata* var. *elliptica* (Briq.) Moldenke, Moldenke repeated the same taxonomic action, not once but four times (Moldenke, 1940: 441; 1942: 310; 1947: 363; 1948: 408), with the last three names constituting later isonyms, which are disregarded by the Code (McNeill et al., 2012: Art. 6, Note 2). To add confusion to this, Moldenke (1942: 310) committed a typographic error between varieties *platyphylla* and *elliptica*, which he later corrected (1947: 363). There are three sheets at G collected by Balansa, number 1016, with a collection date of 1874, from Paraguay, that correspond to *A. virgata* var. *elliptica*. There is no

indication of pro parte on these three sheets, although the pro parte designation could be traced to three additional sheets at G for the collection *Balansa 1016*, each noted as “Isotypus, *Malabaila carvifolia* Boiss. & Balansa,” with “validated determination” to *Peucedanum palimbioides* Boiss., Apiaceae, from Turkey [G SIB #s 271723/1, 2, 3]. Thus the pro parte designation for the type of *Lippia virgata* var. *elliptica* Briq. referred to Balansa’s collection number 1016 mixed with another taxon in a different family, rather than any confusion on Balansa’s part for varieties in *L. virgata*. Consequently, a mixed collection for *Balansa 1016* exists at G that consists of at least six sheets for *Balansa 1016*, three for *L. virgata* var. *elliptica* and three for *Malabaila carvifolia* (Apiaceae), with all six sheets indicated as type material.

Selected specimens examined. ARGENTINA. **Chaco:** 1° de Mayo, Colonia Benítez, *Venturi 7897* (SI). **Corrientes:** Ituzaingó, Rápidos del Apipé, *Cabrera 28959* (SI); s. loc., *Burkart 6923* (SI). **Entre Ríos:** Diamante, Puerto, *Bacigalupo 1659* (SI). **Formosa:** Pirané, ferrocarril, *Krapovickas 1136* (SI). **Jujuy:** El Carmen, Pampa Blanca, *Kiesling 1654* (SI). **Misiones:** Capital, Posadas, *F. M. Rodríguez 97* (SI). **Salta:** Metán, El Tunel, *Saravia Toledo 1929* (SI). **Santiago del Estero:** Carlos Pellegrini, co. Del Remate, *Venturi 5860* (SI). **Tucumán:** Burruyacu, Alto de Medina, *Venturi 2692* (SI). BOLIVIA. **Chuquisaca:** El Salvador, El Huare, *Saravia Toledo 10339* (SI). **Santa Cruz:** Cordillera, Camiri, *Ferrucci 2706* (SI). **Tarija:** Villa Monetes, Qda. de Tampinta, *Krapovickas 19383* (SI). PARAGUAY. **Alto Paraná:** Fiebrig 6151 (SI). **Boquerón:** Colonia Menno, rio Verde, *Vanni 1858* (SI). **Caaguazú:** rte. 2, Km. 122, *Zardini 10633* (SI). **Central:** Yaguarón, *Krapovickas 12255* (SI). **Chaco:** Carnachini, *Rojas 7216* (SI). **Cordillera:** San Bernardino, *Hassler 263* (SI). **Guairá:** Colonia Independencia, serranía Ybytumesú, *Schinini 14* (SI). **Misiones:** San Ignacio, *Burkart 18241* (SI). **Nueva Asunción:** 60 km W Est. La Patria, *Nicora 9758* (SI). **Paraguarí:** Cerro Mbatoví, *Zardini 4451* (SI). **San Pedro:** Villa Primavera, *Woolston 793* (SI).

28b. *Aloysia virgata* (Ruiz & Pav.) Pers. var. *virgata*.

Aloysia urticoides Cham., Linnaea 7: 238. 1832. *Lippia urticoides* (Cham.) Steud., Nomencl. Bot. 2: 54. 1841. TYPE: Brazil. s. loc., s.d., *F. Sellow s.n.* (lectotype, designated by Siedo [2010: 201], G [barcode] G00208721 not seen, G image!; isolectotypes, G [bc] G00386463 not seen, G image! GH!, HAL [bc] HAL0098258 not seen, HAL image!, K [bc] K000487003 not seen, K image!, NY [bc] NY0136532 not seen, NY image!, P [bc] P00713758 not seen, P image!, US not seen, US image!).

Lippia urticoides (Cham.) Steud. var. *laxa* Chodat, Bull. Herb. Boissier, ser. 2, 2: 819. 1902. *Lippia virgata* var. *laxa* (Chodat) Briq., Annuaire Conserv. Jard. Bot. Genève 7–8: 304. 1904. *Aloysia virgata* var. *laxa* (Chodat) Moldenke, Phytologia 1: 95. 1934. TYPE: Paraguay. Sierra de Mbaracayu, Oct. 1898–1899, *E. Hassler 5206* (holotype, G [barcode] G00306073 not seen, G image!; isotypes, G [bc] G00400306 not seen,

G image!, K [bc] K000545989 not seen, K image!; P [bc] P00753761 not seen, P image!, P [bc] P00753760 not seen, P image!, P [bc] P02851825 not seen, P image!, MPU [bc] MPU012512 not seen, MPU image!, UC [bc] UC935077 not seen, UC image!).

Aloysia virgata var. *argutedentata* Moldenke, Phytologia 55(4): 232. 1984. TYPE: Argentina. Santiago del Estero, C. Pellegrini, cerro del Remote, 14 Jan. 1928, *S. Venturi 5764* (holotype, US [barcode] US00118883 not seen, US image!; isotypes, A [bc] A00354571 not seen, A image!, F [bc] F0092407F not seen, F image!, GH [bc] GH00354572 not seen, GH image!, NY [bc] NY01365328 not seen, NY image!, S11-10466 not seen, S image!, SI [bc] SI3404!).

Shrubs with elliptic leaf blades, longer than wide, with acute apex, and acute to subobtuse base. Glabrous ovary.

Distribution and habitat. *Aloysia virgata* var. *virgata* grows in Bolivia, Paraguay, Peru, southern Brazil, and northern Argentina. It has been observed in open fields and sometimes in sandy soils.

Discussion. *Aloysia virgata* is distinguished by its lax, subpendulous florescences, solitary or two to five, sometimes seven, per leaf axil. It is similar to *A. peruviana* and *A. scorodonioides*. However, it is contrasted by its leaf margins minutely serrate or crenate and shorter corollas, less than 4 mm, contrasted with leaf margins notoriously crenate or dentate, and corollas more than 4 mm long in these two last taxa.

There is a certain phenotype of *Aloysia virgata* var. *virgata* found in southern Brazil (Mato Grosso do Sul, Paraná, Santa Catarina) and northeastern Argentina (Misiones), with large leaves to 15 cm long, with narrowly elliptic blades and an acute apex, and long florescences to 15–20 cm in fructification. Generally, there are five to 12 florescences per node, many times reiterated in successive nodes, which makes the plant look like a feather duster. Siedo (2006) referred to this form as *A. virgata* var. *urticoides* (Cham.) Siedo, based upon *A. urticoides* Cham.; however, Siedo’s variety was never validly published and is an ined. name. In the present treatment we consider this to fall within the range of morphological variation of *A. virgata* s. str.

Selected specimens examined. ARGENTINA. **Catamarca:** Ruta Prov. 2, entre Icaño y Ancasti, *Biurrun 8133* (SI). **Chaco:** Ruta 11, 54 millas N de Resistencia, *Cordo 77-A-96* (SI). **Corrientes:** San Miguel, 12 km. N de San Miguel, Ruta 17, *Ahumada 2375* (SI). **Formosa:** Ing. Juárez, *Burkart 20287* (SI). **Jujuy:** San Pedro, Sierra de Zapla, *Burkart 11993* (SI). **Misiones:** El Dorado, ruta 17, a 15 km de El Dorado, *Cabrera 28951* (SI). **Salta:** La Viña, Dique Cabra Corral, *Cabrera 29734* (SI). **Tucumán:** Tafí Viejo, Tapia, *Rodriguez 545* (SI). BOLIVIA. **Beni:** San Borja, *Beck 12734* (SI). **Chuquisaca:** Siles, *Beck 9364* (SI). **La Paz:** Nor/Sud

Yungas, Puente Villa, *Beck* 4791 (SI). **Santa Cruz:** Cordillera, Alto Parapetí, *Michel* 115 (SI). BRAZIL. s. loc., *Saint Hilaire* s.n. (MVM). **Bahia:** s. loc., *Blanchet* 1330 (SI). **Mato Grosso do Sul:** Bela Vista, *Schinini* 1993 (SI). **Minas Gerais:** s. loc., *Claussen* 6087 (SI). **Paraná:** Perola D'Oeste, *Hatschbach* 22629 (SI). **Rio de Janeiro:** entre Macuco & Santa María Magdalena, *Santos* 2043 (SI). **Santa Catarina:** Cambará, aguas de Chapecó, *Klein* 5604 (SI). **São Paulo:** Porto Feliz, *Morello* 49 (SI). PARAGUAY. **Alto Paraná:** Pto. Bestosi, *Rojas* 7987 (SI). **Caaguazu:** ruta 2, *Zardini* 10579 (SI). **Cordillera:** Tobatí, "Ybytu Silla," *Zardini* 27301 (SI). **Guaira:** Ybytyruzú, Cerro Polilla, *Zardini* 13918 (SI). **Paraguarí:** Choló, *Eskuche* 6247 (SI). PERU. **Cuzco:** Santa Ana, *Cook* 1484 (US). **Junín:** Pte. Herreria, *Schunke Vigo* 6202 (US). **San Martín:** Puente Colombia, entre Tarapoto y Juanjui, *Ferreira* 17541 (US).

DOUBTFUL TAXON

Aloysia dodsoniorum Moldenke, *Phytologia* 50: 308. 1982. TYPE: Ecuador. Guayanas: Capeira, Gauyaquil to Daule, 15 Sep. 1981, *C. H. Dodson & P. M. Dodson* 11224 (holotype, TEX-LL [barcode] LL00374937 not seen, TEX-LL image!).

No further material, apart from the type specimen, could be found for this taxon. The type material resembles a *Lippia*.

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- Appendix 1. Accepted species and varieties of *Aloysia*.
1. *Aloysia arequipensis* Siedo
 2. *Aloysia brasiliensis* Moldenke
 3. *Aloysia castellanosi* Moldenke
 4. *Aloysia catamarcensis* Moldenke
 5. *Aloysia chamaedryfolia* Cham.
 6. *Aloysia citrodora* Paláu
 7. *Aloysia cordata* Siedo
 8. *Aloysia crenata* Moldenke
 9. *Aloysia deserticola* (Phil.) Lu-Irving & N. O'Leary
 10. *Aloysia dusenii* Moldenke
 11. *Aloysia fiebrigii* (Hayek) Moldenke
 - 12a. *Aloysia gratissima* (Gillies & Hook. ex Hook.) Tronc. var. *angustifolia* (Tronc.) Botta
 - 12b. *Aloysia gratissima* var. *chacoensis* (Moldenke) Botta
 - 12c. *Aloysia gratissima* (Gillies & Hook. ex Hook.) Tronc. var. *gratissima*
 - 12d. *Aloysia gratissima* var. *schulziana* (Moldenke) Botta
 13. *Aloysia hatschbachii* Moldenke
 14. *Aloysia herrerae* Moldenke
 15. *Aloysia oblanceolata* Moldenke
 16. *Aloysia ovatifolia* Moldenke
 17. *Aloysia peruviana* (Turcz.) Moldenke
 18. *Aloysia polygalifolia* Cham.
 19. *Aloysia polystachya* (Griseb.) Moldenke
 20. *Aloysia pulchra* (Briq.) Moldenke
 21. *Aloysia riojana* (Hieron. ex Moldenke) Lu-Irving & N. O'Leary
 22. *Aloysia salsoloides* (Griseb.) Lu-Irving & N. O'Leary
 23. *Aloysia salviifolia* (Hook. & Arn.) Moldenke
 - 24a. *Aloysia scorodonioides* (Kunth) Cham. var. *hypoleuca* (Briq.) Moldenke
 - 24b. *Aloysia scorodonioides* var. *mathewsii* (Briq.) Moldenke
 - 24c. *Aloysia scorodonioides* var. *scorodonioides*
 25. *Aloysia tarapacana* (Botta) Lu-Irving & N. O'Leary
 26. *Aloysia trifida* (Gay) Lu-Irving & N. O'Leary
 27. *Aloysia velutina* Siedo
 - 28a. *Aloysia virgata* (Ruiz & Pav.) Pers. var. *platyphylla* (Briq.) Moldenke
 - 28b. *Aloysia virgata* var. *virgata*
- Appendix 2. Index to collectors.
- Collections are listed alphabetically by collector's last name. The number in parentheses, after the collector's number, corresponds to the species number in the species list (Appendix 1).
- Ahumada, O.** 8 (12c), 986 (28a), 2375 (28b), 4458 (28b), 4665 (12c), 9002 (12c). **Alberti, F. R.** 619 (12c), 1232 (12c). **Aliscioni, S. S.** 692 (12a). **Alonso, E.** 548 (12b). **Arenas, P.** 148 (15), 257 (19), 276 (6), 351 (6), 370 (15), 428 (22), 444 (6), 664 (12b), 927 (11), 1023 (6), 1085 (12a), 1879 (12b), 1916 (19), 1918 (6), 2330 (12d), 3266 (19), 3465 (19), 20262 (19). **Argañarás, J. L.** 61 (12b). **Asplund, E.** 6533 (24b). **Bacigalupo, N.** 1659 (28a). **Baer, G. A.** 2 (12c), 31794 (16). **Báez, J. R.** 3 (12c), s.n. (12b). **Balegno, B.** 971 (12a), 1068 (12a), 1410 (12a), 1584 (12c). **Barkley, F. A.** 214 (12c), s.n. (12c). **Barriónuevo, A.** s.n. (12a). **Bartlett, H. H.** 19200 (12c), 19543 (12c), 19687 (12d), 19942 (12c), 20004 (12c), 20076 (12c), 20513 (3), 20548 (9), 20573 (3), 20602 (12c). **Beck, S.** 463 (12c), 874 (15), 3530 (24a), 4791 (28b), 6039 (24c), 9364 (28b), 9428 (24b), 12734 (28b), 14132 (22), 21555 (9), 26988 (11). **Bertoni, M.** 761 (12d), 3617 (20), 98421 (20). **Biganzoli, F.** 1414 (20). **Biloni, A.** 16624 (28b). **Biloni, J. S.** 6255 (16), 6671 (22). **Biurrun, F.** 650 (12c), 718

(16), 974 (4), 1214 (12c), 1250 (16), 1302 (16), 2569 (12d), 2774 (6), 4002 (12d), 4080 (19), 4250 (19), 4272 (16), 4688 (6), 4700 (4), 4701 (16), 4740 (26), 4963 (9), 4996 (16), 5042 (3), 5639 (9), 5819 (3), 5980 (21), 5998 (4), 6370 (22), 6392 (12d), 7693 (21), 7696 (21), 7705 (21), 7706 (26), 7710 (21), 8133 (28b). **Blanchet, J.** 1330 (28b). **Bocco, M. E.** 821 (12c). **Boelcke, O.** 1249 (12c). **Boffa, P.** s.n. (12b). **Bonifacino, M.** 1953 (5). **Botta, S. M.** 116 (12c), 273 (12c), 364 (22), 685 (4), 695 (3). **Brescia, R.** 4269 (20). **Bridges, E.** 1346 (23). **Brizuela, A.** 90 (19), 181 (16), 386 (12c), 389 (19), 437 (12c), 550 (12c), 882 (12c), 1082 (19), 1180 (12c). **Brown, A.** 1610 (12d). **Bruch, C.** s.n. (12c). **Buchtien, O.** 3240 (24c). **Buratovich, F.** 219 (12d), 941 (12c). **Burkart, A.** 3083 (12c), 4140 (12c), 6923 (28a), 6928 (12c), 8486 (12c), 11966 (22), 11993 (28b), 12536 (21), 12540 (21), 12542 (6), 12543 (16), 12545 (16), 12549 (4), 13195 (12d), 13856 (12c), 13858 (12c), 13968 (16), 14201 (20), 14209 (20), 15281 (20), 15834 (12c), 18002 (12c), 18241 (28a), 20226 (19), 20287 (28b), 21361 (12a), 22066 (3), 23796 (12c), 23800 (12a), 23805 (12a), 26347 (12c), 26348 (12c), 26594 (12c), 27051 (12c), 27876 (12c), 28067 (12a), 28074 (12c), 29450 (12c), 29465 (12c), 29641 (16), 30574 (16), 30593 (24c), 30595 (12d), 30596 (28b), 30606 (12d), 30608 (12c).

Cabezas, V. 23192 (12c). **Cabrera, A. L.** 3046 (12c), 4368 (12c), 7209 (12c), 7716 (22), 8192 (12c), 9016 (22), 12183 (12c), 13252 (22), 14241 (24c), 14633 (12d), 15711 (24b), 16695 (6), 16783 (4), 16877 (6), 18475 (12c), 19245 (12c), 20325 (12c), 20988 (24b), 21092 (12d) 22438 (22), 23330 (28a), 24637 (6), 24648 (12c), 27399 (22), 27962 (24b), 28063 (16), 28331 (20), 28485 (20), 28634 (20), 28743 (20), 28870 (28b), 28951 (28b), 28959 (28a), 28973 (12c), 28989 (20), 29017 (12c), 29029 (12c), 29062 (20), 29104 (28a), 29106 (8), 29117 (20), 29187 (28b), 29529 (12c), 29554 (12c), 29588 (16), 29603 (12c), 29616 (12c), 29632 (12c), 29664 (12a), 29670 (12c), 29727 (24b), 29729 (24c), 29731 (12c), 29734 (28b), 29736 (12d), 29745 (24c), 29746 (12c), 29828 (12c), 29961 (24c), 30346 (12d), 31018 (12d), 31725 (22), 31735 (22), 31792 (9), 32301 (28a), 32345 (12c), 32474 (22), 32746 (28a), 33665 (24c), 34018 (28a), 34101 (24c). **Calderón, C. E.** 991 (12a), 1243 (12c), 1386 (12c). **Cano, E.** 724 (12c), 1971 (12c). **Cantino, P.** 327 (12c), 557 (12c), 559 (12c), 693 (3), 734 (16). **Carette, E.** 3046 (12c), 3877 (12c). **Castellanos, A.** 585 (12a), 623 (12a), 11669 (19), 19062 (12c), 19615 (12a), 28/327 (6), 28/331 (16), 33887 (19), 33892 (12a), 33894 (16). **Castillon, L.** 943 (6). **Cerón** 12387 (12c). **Cerrate, E.** 1282 (1). **Cialdella, A.** 218 (3), 407 (22). **Claussen, P.** 6087 (28b). **Cocucci, A.** 3277 (25), 3366 (11). **Cook** 247 (24b), 1484 (28b). **Cordini, R. I.** 60 (12b). **Cordo, H.** 77-A-33 (12c), 77-A-49 (12c), 77-A-50 (12a), 77-A-93 (12a), 77-A-94 (12c), 77-A-96 (28b), 77-A-101 (12b), 77-A-102 (28b), 77-A-160 (12c), 77-B-11 (12c), 77-B-66 (28b), 77-B-70 (12c), 77-B-82 (12c), 77-B-83 (19), 77-B-88 (12c), 77-C-21 (12c), 77-C-33 (12c), 77-D-45 (12d), 77-D-46 (12c), 77-D-47 (12c), 78-A-39 (28a), 78-A-41 (12a), 78-A-42 (12b), 78-A-43 (12d), 78-A-44 (12c), 78-A-45 (12d), 78-A-46 (12d), 78-A-48 (24c), 82-A-24 (22), 89-A-93 (12c). **Correa, A.** 209 (12c), 238 (12c), 4318 (4), 18073 (12c). **Correa, J. B.** 26 (12c). **Corzo, R.** 777 (19). **Costa, M.** 6 (7). **Cozzo, D.** s.n. (12a). **Crespo, S.** 26457 (12c). **Cristóbal, C. L.** 1649 (12c). **Cuezso, A. R.** 971 (19), 1656 (3), 9362 (12c), 9498 (12c).

Davis, E. 1757 (14). **Dawson, G.** 3340 (6), 3432 (16). **De la Sota, A. V.** 198 (12b), 261 (12c), 447 (12c), 458 (12c), 580 (12c), 4236 (12c). **De la Vega, R.** 26 (6), 44 (6). **Deginani, N.** 1375 (20). **Del Castillo, A.** 451 (12c). **Del Puerto** 6053 (20). **Dematteis, M.** 1531 (20). **Denham, S.** 333 (12c). **Descole, H. R.** 3330 (28b). **Devoto, F.** 1142 (24c), 1566 (12c), 2208 (12c), 2257 (12c), 3427 (24c). **Dier, L.** 148 (22). **Dillon, M.**

4544 (27), 6018 (9). **Donadio, S.** 177 (19). **Donovan** P978 (17). **Drake, J.** s.n. (24c). **Dunn, D.** 20552 (12c).

Ekman, E. L. 1999 (20), 2000 (20), 2004 (5). **Escobar, H.** 233 (25). **Eskuche, U.** 6247 (28b). **Eukontes, J.** 534 (20). **Eyerdam, W.** 22363 (12c), 23408 (12c).

Fabris, H. A. 2729 (12c), 2994 (12b), 3081 (12c), 3546 (12c), 6036 (22), 6336 (22), 7954 (12c), 7989 (28b), 8121 (6). **Ferreira, R.** 755 (17), 759 (17), 7013 (24a), 7021 (24a), 12952 (17), 17541 (28b). **Ferrucci, M.** 2659 (15), 2706 (28a). **Fiebrig, K.** 3040 (11), 5904 (20), 6151 (28a). **Fortunato, R.** 1269 (12c), 2339 (12c), 5040 (12c), 5091 (16), 5950 (12c), 6628 (12c). **Forzza, R. C.** 1977 (12c), 1978 (6). **Frenguelli, J.** 19 (12c). **Fries, R.** 746 (22).

Garaventa 7092 (12c). **García, E.** 1209 (9). **García, P.** 814 (12a). **Gentry, H.** 36089 (17), 44821 (17), 70190 (24c). **Gerold, H.** 161 (6). **Giardelli, M. L.** 25 (12a), 418 (12a), 19542 (12c). **Giberti, G.** 825 (22). **Golbach, R.** 9 (12c). **Gomez** 28/770 (19). **Guaglianone, R.** 220 (20), 599 (12c), 956 (20) 2071 (12c), 2787 (12c).

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Ochoa, C. 710 (14). **O'Donell, C. A.** 3159 (12c), 4366 (12c), 5377 (12c). **Okada, K.** 2747 (12c). **Olea, D.** 78 (6), 99 (12d). **Olmstead, R.** 2001-184 (16), 2004-109 (12c), 2004-125 (28b), 2004-129 (20), 2004-133 (28b), 2007-13 (6), 2007-13 (6), 2007-52 (22), 2007-68 (28a), 2007-82 (4), 2007-82 (4), 2009-30 (14), 2009-40 (24a), 2009-45 (17), 2009-8 (27), 2010-217 (10).
Pachano, A. 120 (24c). **Parodi, L. R.** 14244 (12c). **Pastore, F.** 2031 (12c). **Paula-Souza, J.** 6989 (12c), 7623 (22), 7697 (22), 7796 (12d), 8122 (28a). **Pedersen, T. M.** 614 (12c), 874 (12c), 5564 (12c), 6428 (12c), 8261 (12c), 11796 (19), 15295 (4). **Pennell, M.** 14438 (24c). **Pensiero, J.** 1722 (12c), 4249 (12c), 5640 (12c), 5707 (12c), 7426 (12d), 7450 (12c). **Perez Moreau, R.** 13577 (12a). **Pfsister** 8318 (23). **Pierotti, S.** 16 (12a). **Pittier, H.** 970 (6). **Pozner, R.** 144 (4). **Prado, D. E.** 107 (12c). **Prina, A.** 2696 (12c). **Pringle, C.** s.n. (12c). **Pujalte, J. C.** 133 (9).
Quarín, C. 2117 (20). **Queiroz, L. P.** 13358 (12d), 13465 (22).
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Taylor, A. 11607 (26). **Terribile, M.** 376 (12b), 418 (6). **Thode, V.** 157 (13), 398 (18). **Torrico** 107 (12d). **Troiani, H.** 558 (12c). **Troncoso, N.** s.n. (12c), 299 (12c), 1062 (12c), 1253 (12c), 1277 (12c), 1824 (12d), 1826 (12c), 1856 (12c), 1857 (12c), 1859 (12c), 1860 (12c), 1861 (6), 1893 (6), 1895 (6), 1896 (6), 1897 (6), 1898 (6), 1910 (12b), 1929 (6), 1930 (12c), 1931 (6), 1989 (12c), 2496 (12a), 20589 (12c).
Ulibarri, E. 332 (4), 333 (12c), 679 (9), 906 (16), 950 (4), 1481 (9).
Vanni, R. 1830 (12c), 1858 (28a), 2410 (12d). **Varela** 675 (12c). **Vargas, C.** 248 (14), 594 (24b), 3692 (24c), 12671 (1). **Vattuone, I. C.** 71 (12c). **Velarde Nuñez, O.** 301 (17). **Venturi, S.** 834 (12c), 849 (24c), 2692 (28a), 3756 (19), 3963 (16), 4262 (6), 4885 (22), 5860 (28a), 7458 (28a), 7897 (28a), 8144 (22), 8300 (22), 10579 (24b). **Vervoost, F.** 498 (12c), 688 (22), 4318 (4), 4476 (22), 8642 (12c). **Vignati, M.** 977 (12c). **Villafañe, M.** 342 (12c), 464 (12c), 558 (12c), 693 (12a), 751 (12a), 776 (12c).
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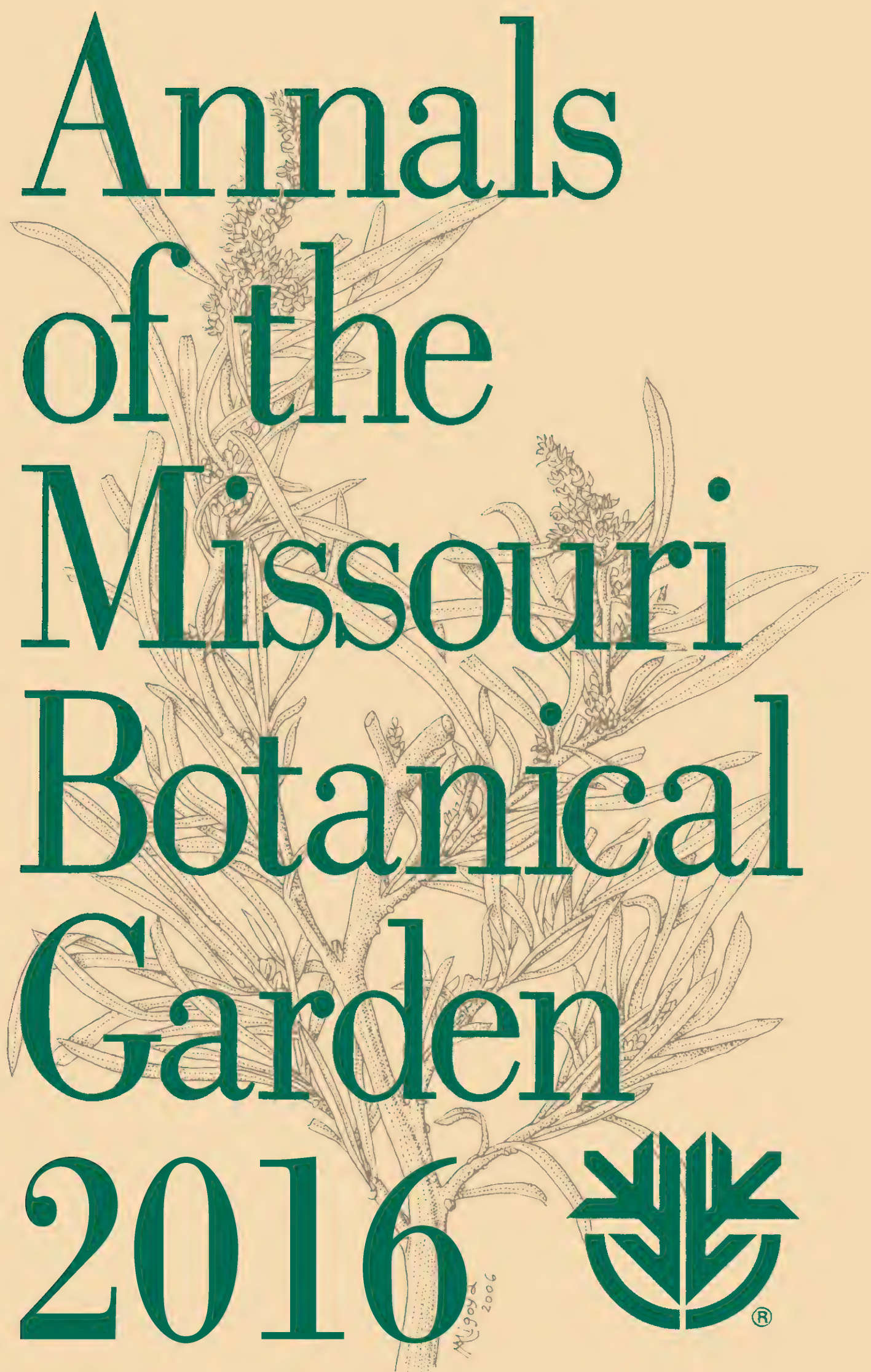
Appendix 3. List of taxa newly synonymized in the present work.

Aloysia ayacuchensis Moldenke [= *A. herrerae* Moldenke]

<i>Aloysia axillaris</i> J. R. I. Wood [= <i>A. scorodoniioides</i> var. <i>hypoleuca</i> (Briq.) Moldenke]	<i>Aloysia leptophylla</i> Moldenke [= <i>A. scorodoniioides</i> (Kunth.) Cham. var. <i>scorodoniioides</i>]
<i>Aloysia depressa</i> Ravenna [= <i>A. scorodoniioides</i> var. <i>hypoleuca</i> (Briq.) Moldenke]	<i>Aloysia minthiosa</i> Moldenke [= <i>A. peruviana</i> (Turcz.) Moldenke]
<i>Aloysia floribunda</i> M. Martens & Galeotti [= <i>A. gratissima</i> (Gillies & Hook) Tronc. var. <i>gratissima</i>]	<i>Aloysia reichei</i> Moldenke [= <i>A. trifida</i> (Gay) Lu-Irving & N. O’Leary]
<i>Aloysia gratissima</i> var. <i>oblanceolata</i> Moldenke [= <i>A. oblanceolata</i> Moldenke]	<i>Lippia fonckii</i> Phil. [= <i>A. trifida</i> (Gay) Lu-Irving & N. O’Leary]

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TAXONOMIC REVISION OF
GERANIUM SECT. *POLYANTHA*
(GERANIACEAE)¹

Carlos Aedo²

ABSTRACT

Geranium L. sect. *Polyantha* Reiche (Geraniaceae) consists of seven species. The highest diversity of the group is located in southwestern China with five endemic species. One species is found in the Himalaya, and another is located in the mountains of Burma. In contrast with some regional treatments, I have synonymized *G. ascendens* Z. M. Tan to *G. moupinense* Franch., and *G. platylobum* (Franch.) R. Knuth to *G. hispidissimum* (Franch.) R. Knuth. Micromorphological features of indumentum, pollen, and mericarps were investigated by SEM. The presence of pollen with *Erodium* L'Hér.-type exine ornamentation is confirmed for all species of the section. A new key is provided, as well as new and detailed descriptions. Each species is illustrated and mapped, and three lectotypes are designated.

Key words: Asia, Geraniaceae, Himalaya, monograph, morphology, taxonomy.

Geranium L. (Geraniaceae) is a genus of medium size with, at the present time, an estimated 325 species distributed throughout most of the world except lowland tropical areas. The difficulty of preparing monographic treatments of large genera is well known (Frodin, 2004) and applies to medium-sized genera as well. As part of an ongoing project to revise this genus worldwide, the initial strategy was to review sections or subgenera that were well characterized morphologically (Aedo, 1996, 2001, 2003; Aedo et al., 1998, 2002, 2003, 2005a, 2005b, 2007).

A complementary strategy has been to revise groups by geographical areas, for example, the species of the New World (Aedo, 2012) and those of the Pacific area (Aedo, 2016). Among the groups well characterized morphologically but not yet fully revised is *Geranium* subg. *Robertium* (Picard) Rouy. According to Yeo (1984), *Geranium* subg. *Robertium* is recognized by fruit discharge by carpel projection (see under Morphology) and may be divided into eight sections, distributed mainly in Macaronesia, the Mediterranean Basin, and the Himalaya. Among these,

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Geranium sect. *Batrachioidea* W. D. J. Koch and *Geranium* sect. *Divaricata* Rouy were monographed by Aedo et al. (1998), and *Geranium* sect. *Trilopha* Yeo by Aedo et al. (2016). *Geranium* sect. *Anemonifolia* R. Knuth and *Geranium* sect. *Ruberta* Dumort. were studied by Yeo (1973), and *Geranium* sect. *Lucida* R. Knuth and *Geranium* sect. *Unguiculata* (Boiss.) Reiche by Yeo (2004). Some work is still needed, however, to achieve a comprehensive monograph of these last four. The eighth section of the subgenus is *Geranium* sect. *Polyantha* Reiche, which is the subject of the present revision.

Reiche (1890) described *Geranium* sect. *Polyantha* as including three species: *G. polyanthes* Edgew. & Hook. f., *G. umbelliforme* Franch., and *G. tuberaria* Jacquem. ex Cambess.; the latter is currently classified into *Geranium* sect. *Tuberosa* Boiss. of the subgenus *Geranium* (Yeo, 1984; Aedo & Estrella, 2006). Knuth (1912) accepted three species in *Geranium* sect. *Polyantha*: *G. moupinense* Franch., *G. polyanthes*, and *G. umbelliforme*. However, the four additional species, *G. hispidissimum* (Franch.) R. Knuth, *G. strictipes* R. Knuth, *G. platylobum* (Franch.) R. Knuth, and *G. strigosum* Burm. f., are classified by Knuth (1912) into *Geranium* sect. *Palustria* R. Knuth. Yeo (1975, 1984) transferred *G. strigosum* to *Geranium* sect. *Polyantha* and synonymized *G. strigosum* to *G. strictipes* and *G. platylobum* to *G. hispidissimum*. In this work, the group is configured as it is currently understood.

Yeo (1992) recognized six species from southwestern China in the context of a revision of the genus for this area: the previously mentioned *Geranium polyanthes*, *G. umbelliforme*, *G. moupinense*, *G. strictipes*, *G. hispidissimum*, and *G. ascendens* Z. M. Tan. The latter, a species described by Tan (1990), is currently considered as a synonym of *G. moupinense* (Xu et al., 1998; Xu & Aedo, 2008). In their treatment of the genus for the *Flora Reipublicae Popularis Sinicae*, Xu et al. (1998) described *Geranium* sect. *Strigosa* C. C. Huang & L. R. Xu to separate *G. hispidissimum*, *G. strictipes*, and *G. platylobum* from *Geranium* sect. *Polyantha*, which was reduced to *G. polyanthes*, *G. umbelliforme*, and *G. moupinense*. The treatment of the genus for the *Flora of China* (Xu & Aedo, 2008) did not provide an infrageneric classification of *Geranium* and recognized five species for this group, synonymizing *G. platylobum* to *G. hispidissimum* and *G. ascendens* to *G. moupinense*. Consequently, an important part of the revision was already advanced (Yeo, 1992; Xu & Aedo, 2008). However, to obtain a comprehensive taxonomic treatment of the section, the two non-Chinese species should be included in the study and all species should be reevaluated.

Additionally, information about nomenclature, types, and descriptions should be updated and unified and maps and drawings should be provided.

Following my recent revisions of several groups of *Geranium*, and keeping in mind the goal of comprehensively monographing the genus, I present here a revision of *Geranium* sect. *Polyantha*.

MATERIALS AND METHODS

This revision is based on 164 herbarium specimens from the following herbaria: A, B, BM, C, CAS, E, G, GH, IBSC, JE, K, KUN, KYO, M, MA, MO, NY, P, PE, US, W, WRS, and WU. An index of numbered collections is presented in Appendix 1.

Scored for the description of the species were 110 characters, 75 qualitative traits, and 35 quantitative traits, as well as seven ratios. At least 15 specimens were scored for each species. Quantitative characters were assessed with a Mitutoyo CD-15CD digital caliper (Mitutoyo, Kawasaki, Japan). The most frequent values are percentiles (between the 25th and 75th percentiles), which are shown without brackets, and the extreme values are enclosed in brackets. All measurements were taken from herbarium specimens. The line drawings of leaf laminae and petals show the adaxial surface unless stated otherwise. In the descriptions and key, the length of the sepal does not include the length of the mucro.

For SEM, samples were glued to aluminum stubs, coated with 40–50 nm of gold, and examined with a JEOL-TSM T330A (JEOL USA Inc., Peabody, Massachusetts) SEM at 15 kV.

MORPHOLOGY

All species of *Geranium* sect. *Polyantha* are perennial herbs with a more or less vertical rootstock. The stem is usually well developed, erect, or ascending and branched.

The following types of hairs have been detected in the species of *Geranium* sect. *Polyantha*. All of these hairs are simple and uniseriate (Theobald et al., 1979). According to Payne (1978), hairs 1 and 2 belong to the “subulate” type. The hair types are: (1) Short eglandular (0.1–0.3 mm), unicellular hairs, smooth or papillose, more or less uncinata (Fig. 1A); these occur in a variable frequency in all species, mainly in the inflorescences. (2) Long eglandular (0.2–3.3 mm), unicellular hairs, smooth or papillose, patent (Fig. 1B); these occur in a variable frequency in all species, at least in the inflorescences. (3) Glandular hairs with a foot consisting of cylindrical or decussate cells (Fig. 1C); these occur in all species on almost all structures of a plant. (4) Plane,

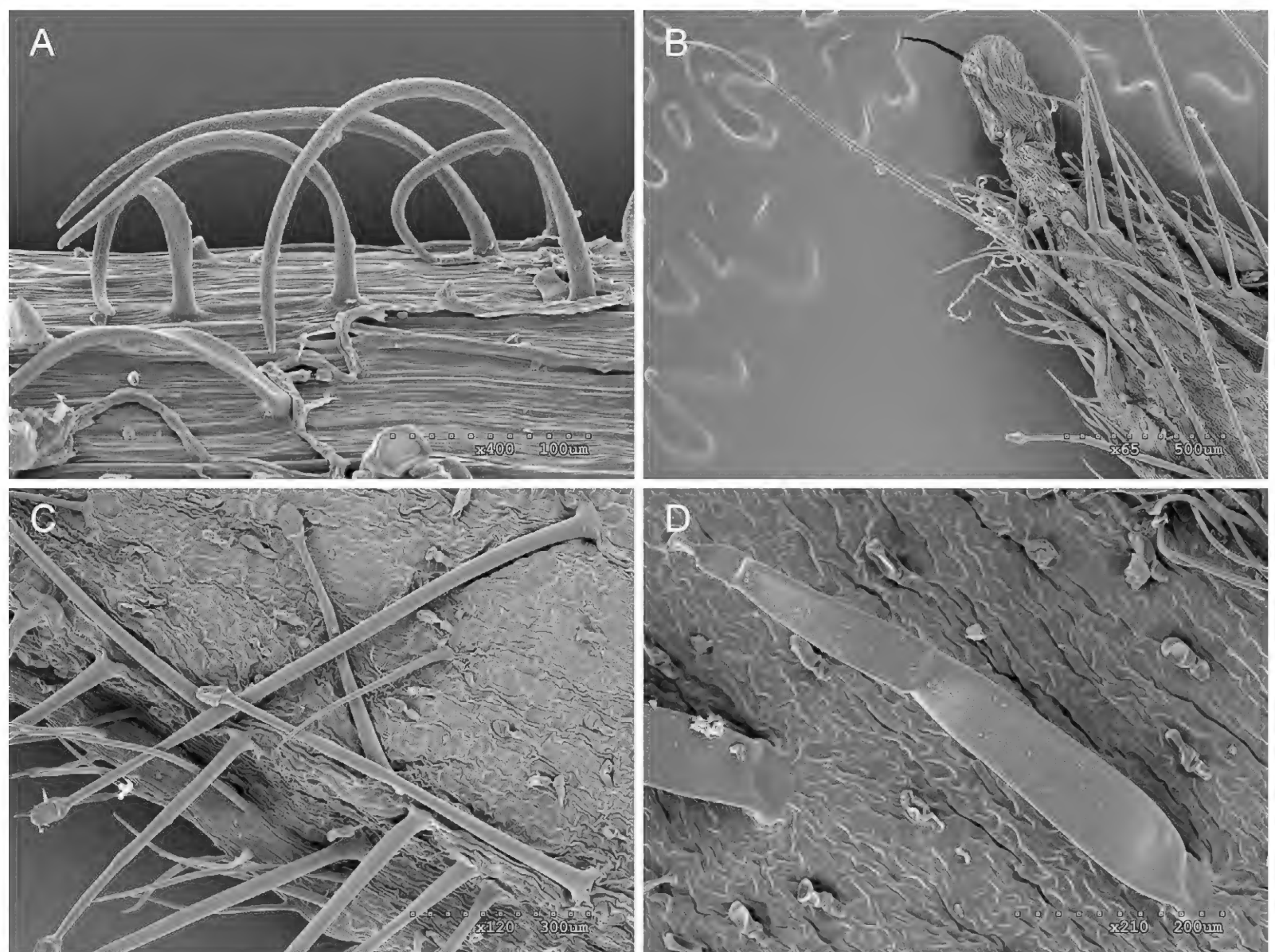


Figure 1. SEM photographs showing hair types found in *Geranium* L. sect. *Polyantha* Reiche. —A. Peduncle of *G. strictipes* R. Knuth showing short eglandular, uncinata hairs (*D. E. Boufford et al.* 33029, MA). —B. Sepal adaxial surface of *G. polyanthes* Edgew. & Hook. f. showing long eglandular hairs (*Gaoligong Shan Biodiversity Survey* 32158, CAS). —C. Sepal adaxial surface of *G. polyanthes* showing long glandular hairs (*Gaoligong Shan Biodiversity Survey* 32158, CAS). —D. Leaf adaxial surface of *G. nakaoanum* H. Hara showing plane, glandular hairs (*F. Miyamoto* 9410140, E).

glandular hairs (0.4–1 mm), with two to four cells, usually papillose (Fig. 1D); these are restricted to the adaxial surface of the leaves in *G. nakaoanum* H. Hara and to both surfaces in the remaining species of *Geranium* sect. *Polyantha*. This feature, which is shared by other species of *Geranium* subg. *Robertium*, does not occur in either *Geranium* subg. *Geranium* or *Geranium* subg. *Erodioidea* (Picard) Yeo. (5) Short glandular hairs (< 55 μ m), smooth, usually of two cells, but sometimes with a bicellular foot, and present in all species studied here. Because these are evident only at high magnification, they are not included in the descriptions.

The primary division of the leaf is referred to as a “segment”; subsequent divisions are called “lobes.” The basal leaves are usually arranged in a more or less deciduous rosette. Cauline leaves are usually similar in shape to the basal leaves, although they become progressively shorter toward the shoot apex. All species have palmatifid leaves (with the divisions over the middle), polygonal in outline and with five

segments. The leaves of *Geranium favosum* Hochst. ex A. Rich., *G. moupinense*, and *G. nakaoanum* are more deeply divided, with divisions of over three quarters. Leaves of *G. hispidissimum*, *G. strictipes*, *G. wardii* Yeo, and, usually, *G. nakaoanum* are opposite. In *G. polyanthes* and *G. umbelliforme*, the middle cauline leaves are alternate, but the more distal ones are opposite. Finally, only alternate leaves occur in *G. moupinense*. Each leaf has two free stipules, one on each side of the petiole base. The stipules are lanceolate in *G. hispidissimum* and *G. strictipes*, broadly lanceolate in *G. moupinense*, and ovate and obtuse in the remaining species of the section.

The cymules are arranged in a dichasial cyme with monochasial branches in *Geranium hispidissimum*, *G. strictipes*, and *G. wardii*, while in the remaining species the cymules are in a monochasial cyme. *Geranium nakaoanum* has cymules usually 1-flowered. *Geranium polyanthes* and *G. umbelliforme* have part of their cymules grouped in umbel-like aggre-

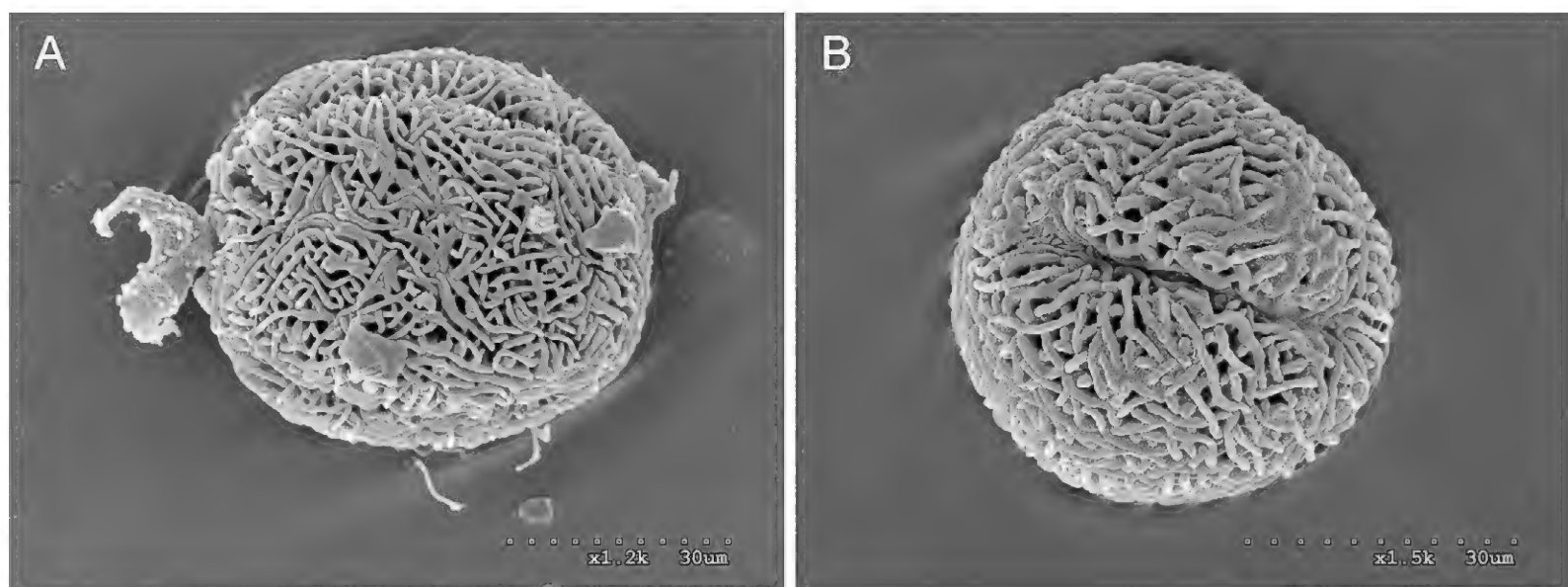


Figure 2. SEM photographs showing pollen grains of *Geranium* L. sect. *Polyantha* Reiche. —A. Pollen grain of *G. moupinense* Franch. (A. David s.n., MA-628480). —B. Pollen grain of *G. nakaoanum* H. Hara (F. Miyamoto 9410140, E).

gates at the top of each branch (usually with more than two flowers per cymule), while the remaining species always have solitary and 2-flowered cymules.

The five sepals form a quincuncial calyx. The two inner sepals are usually smaller and less pubescent than the others. The external surface of each sepal is smooth. The sepals of each species terminate in a distinct mucro.

The five petals are erect-patent, usually with an entire apex and without claw. The petal color is usually purple without any dark basal spots. The petal length is of taxonomic utility to differentiate *Geranium strictipes* from *G. hispidissimum*, the latter having shorter petals. The petals of *G. moupinense*, *G. strictipes*, and *G. umbelliforme* are hairy toward the base on both surfaces and ciliate on the basal margin; in the remaining species petals are usually glabrous on the abaxial surface.

The flowers of *Geranium* sect. *Polyantha* have two whorls of five fertile stamens. The stamens are shorter than the petals. The anthers are dorsifixed and dehisce by longitudinal slits. The filaments are lanceolate, except in *G. nakaoanum*, which has an abruptly narrowed apex. They are hairy on the proximal half and with cilia on the margin.

The pollen of *Geranium* is tricolpate and more or less isodiametric. In most species the exine bears reticulate ornamentation formed by baculate, clavate, or gemmate supratectal elements (Bortenschlager, 1967; Stafford & Blackmore, 1991; Weber, 1996). However, in the species of *Geranium* sect. *Trilopha* (Aedo et al., 2016) and *Geranium* sect. *Polyantha*, the exine shows a striate-rugulose pattern, similar to that found in *Erodium* L'Hér. (Bortenschlager, 1967; El-Oqlah, 1983). It has been confirmed that the pollen of all species of *Geranium* sect. *Polyantha* is of the *Erodium*-type (Fig. 2). This supports the close

relation between *Geranium* sect. *Polyantha* and *Geranium* sect. *Trilopha*, which should be explored more deeply, together with a comprehensive revision of all groups of *Geranium* subg. *Robertium*.

Five hemispheric nectaries are located to the base of and alternate with the petals; they are glabrous in *Geranium nakaoanum*, *G. polyanthes*, *G. umbelliforme*, and *G. wardii*, while in the remaining species they have a tuft of hairs at the top.

The gynoecium comprises five carpels, each with two ovules, of which only one develops into a mature seed. The five styles are fused into a column, divided at the apex into five branches, each of which has a stigmatic surface on the adaxial side.

The type of fruit discharge was the basis for the subgeneric classification of *Geranium* proposed by Yeo (1984). *Geranium* subg. *Erodioidea* is characterized by the “*Erodium*-type” of discharge, in which the entire mericarp, including the coiled awn, is propelled over a short distance. *Geranium* subg. *Geranium* is characterized by the “seed-ejection type” of discharge, in which each single seed is launched by the explosive recurvature of the awn. *Geranium* subg. *Robertium* has a “carpel-projection type” of discharge: the whole mericarp, containing the seed, is dispersed by the propelling force of the explosive recurvature of the awn. The species of *Geranium* sect. *Polyantha* show a discharge of the “carpel-projection type.”

The five carpels of *Geranium* form a syncarpous-lobed ovary maturing into a schizocarp. After fertilization a prominent rostrum develops next to the style. At maturity the carpel shows two parts: (1) a locus containing the seed, named mericarp, and (2) a sterile portion forming a ribbon-like band, which constitutes the rostrum. In some species of *Geranium* the rostrum is gradually narrowed toward the apex, whereas in others it terminates abruptly in a narrow

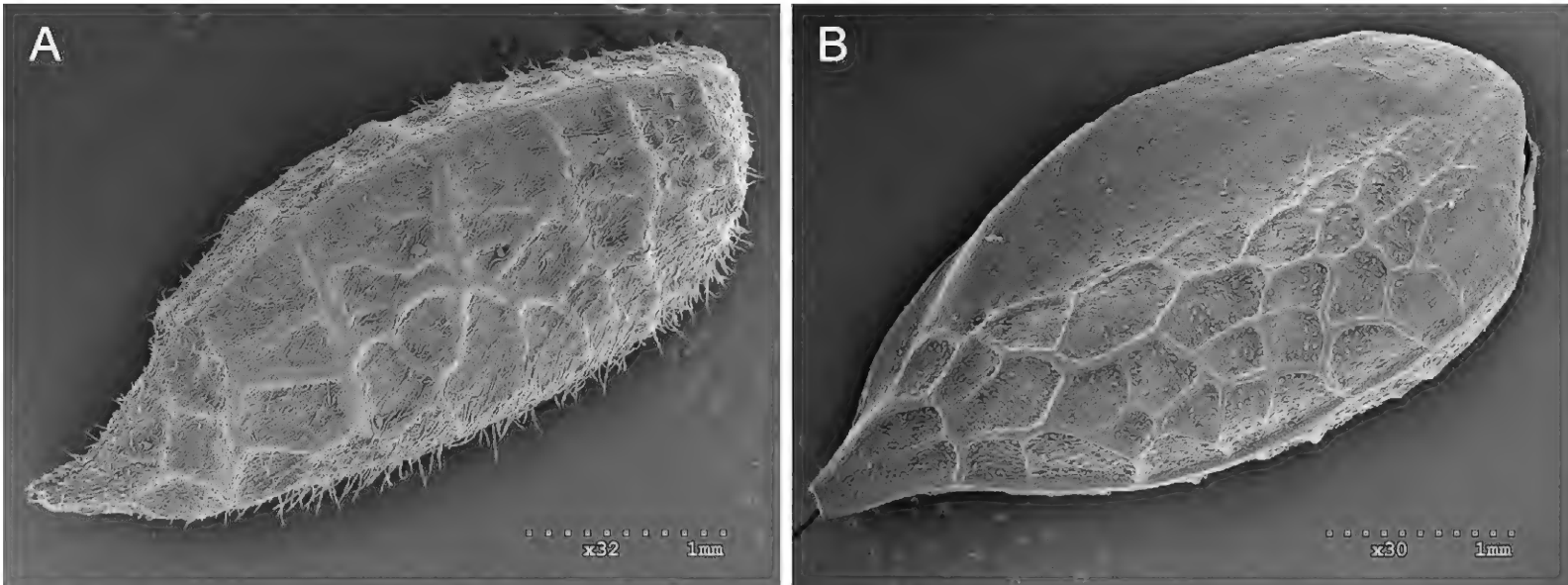


Figure 3. SEM photographs showing mericarps of *Geranium* sect. *Polyantha* Reiche. —A. Lateral view of the mericarp of *G. hispidissimum* (Franch.) R. Knuth (*T. T. Yü 1541*, GH). —B. Lateral view of the mericarp of *G. nakaoanum* H. Hara (*J. H. Haas 2118*, BM).

apex, in which case the apical portion of the rostrum is easily differentiated from the basal portion. Only three species of *Geranium* sect. *Polyantha* (*G. moupinense*, *G. strictipes*, and *G. umbelliforme*) have a well-developed narrowed apex. The five ribbon-like bands of the rostrum are parallel in *Geranium* sect. *Polyantha*. In contrast, in the species of *Geranium* sect. *Trilopha* the rostrum is twisted. The mericarps in *Geranium* sect. *Polyantha* have a slightly reticulate surface and have short eglandular hairs, with the exception of *G. nakaoanum*, which has glabrous mericarps (although some minute glands can be observed at high magnification) (Fig. 3).

The seeds are more or less ellipsoid and slightly compressed. The outer layer of the seed coat has cells with anticlinally thickened walls, forming a finely reticulate surface.

TAXONOMIC TREATMENT

Geranium* sect. *Polyantha Reiche in Engl. & Prantl, Nat. Pflanzenfam. 3(4): 8. 1890. TYPE: *Geranium polyanthes* Edgew. & Hook. f.

Geranium sect. *Strigosa* C. C. Huang & L. R. Xu, Fl. Reipubl. Pop. Sin. 43(1): 47. 1998. TYPE: *Geranium strictipes* R. Knuth.

Perennial herbs. Leaves palmately divided; cauline leaves opposite or alternate; stipules free. Inflorescence in monochasial cyme or dichasial cyme with monochasial branches. Flowers actinomorphic. Sepals lanceolate, erect, not accrescent. Petals usually rounded at

apex, without claw, without basal spot. Stamens not exerted; filaments pilose; pollen of *Erodium*-type. Fruit discharged by carpel projection, each mericarp thrown off explosively with seed in it and awn dropping away at moment of explosion; mericarps reticulate, without basal callus, without basal prong, without strand of fibers, hairy; rostrum not twisted distally. Cotyledons entire.

Distribution and habitat. *Geranium* sect. *Polyantha* occurs from Eastern Himalaya to southwestern China and Burma. The richest areas are the Chinese provinces of Yunnan and Sichuan.

Discussion. *Geranium* sect. *Polyantha* is a group of perennial herbs, well characterized by petals without a basal spot, sepals not accrescent, and pollen of *Erodium*-type. Its fruit has a “carpel-projection type” discharge, as well as reticulate mericarps and a rostrum not twisted distally. *Geranium hispidissimum*, *G. strictipes*, and *G. wardii* share an inflorescence with a dichasial structure and opposite leaves. In contrast, the group comprising *G. polyanthes*, *G. umbelliforme*, and *G. moupinense* has a monochasial inflorescence and alternate leaves (at least in the middle of the shoot). *Geranium nakaoanum* is somewhat intermediate, having a monochasial inflorescence but leaves usually opposite. This species is also the only one in the section showing some other features, e.g., usually 1-flowered cymules, scarce indumentum, and staminal filament shape.

KEY TO THE SPECIES OF *GERANIUM* SECT. *POLYANTHA*

- 1a. Cymules in umbel-like aggregates at the top of each branch.
- 2a. Cymules 2(or 3)-flowered, in dense umbel-like aggregates at apex of each branch, usually without peduncle; rostrum without narrowed apex (sometimes up to 1 mm); petals (7.8)9.3–11.8(14.1) mm..... 4. *G. polyanthes* Edgew. & Hook. f.

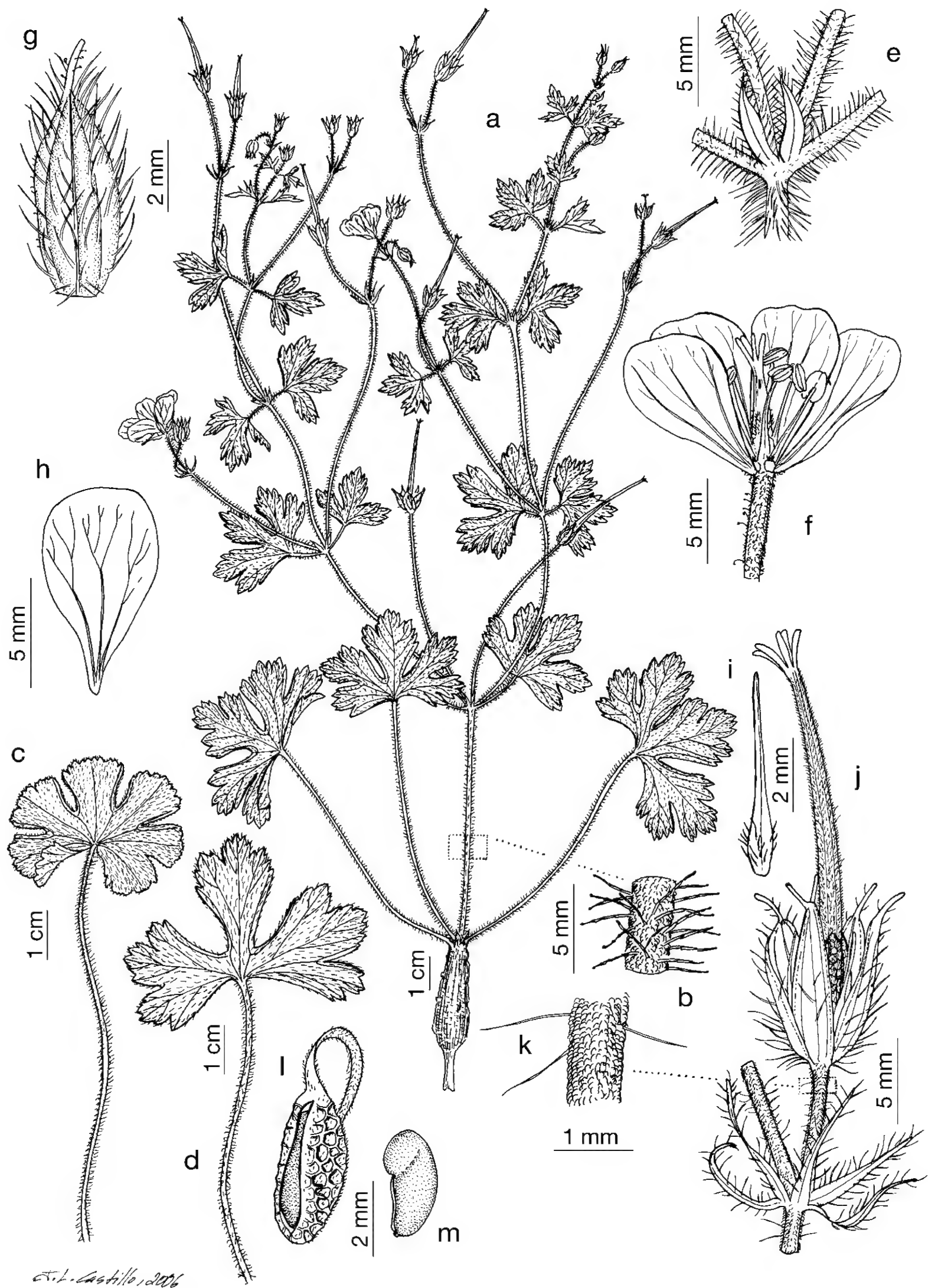


Figure 4. *Geranium hispidissimum* (Franch.) R. Knuth. —A. Habit. —B. Stem indumentum. —C, D. Leaves. —E. Stipules. —F. Flower without sepals. —G. Sepal. —H. Petal. —I. Staminal filament. —J. Fruit. —K. Peduncle indumentum. —L. Mericarp. —M. Seed. A–D, F–H, L, M based on *Qin* 23372 (PE); I–K based on *E. E. Maire* 2577 (E); E based on *E. E. Maire* s.n. (E-216867).

- 2b. Cymules (2- or)3- or 4-flowered, in loose umbel-like aggregates at apex of each branch with peduncles 25–67 mm; rostrum with narrowed apex 2–2.1 mm; petals (13.1)13.8–15.2(16.8) mm 6. *G. umbelliforme* Franch.
- 1b. Cymules solitary.
- 3a. Cymules 1(or 2)-flowered; stem glabrous 3. *G. nakaoanum* H. Hara
- 3b. Cymules 2-flowered; stem \pm hairy 4
- 4a. Basal cauline leaves alternate 2. *G. moupinense* Franch.
- 4b. Basal cauline leaves opposite.
- 5a. Leaf deeply divided (ratio of main sinus length:segment length = [0.70]0.80–0.86[0.89]) 5. *G. strictipes* R. Knuth
- 5b. Leaf not deeply divided (ratio of main sinus length:segment length = [0.55]0.68–0.77[0.81]).
- 6a. Petals (8.6–)9–9.8(–10.6) mm; nectaries hairy at the top; sepal mucro 0.8–2.4 mm; middle segment of the leaf with 9 to 16 lobes 1. *G. hispidissimum* (Franch.) R. Knuth
- 6b. Petals 12.6–13.4 mm; nectaries glabrous; sepal mucro 1.1–1.2 mm; middle segment of the leaf with 7 to 8 lobes 7. *G. wardii* Yeo

1. *Geranium hispidissimum* (Franch.) R. Knuth in Engl., Pflanzenr. IV. 129 (Heft 53): 183. 1912. *Geranium strigosum* var. *hispidissimum* Franch., Pl. Delavay. 113. 1889. TYPE: China. Yunnan: ad collum montis Hee-chan-men, 26°06'N, 99°57'E, 15 July 1887, *P. J. Delavay s.n.* (lectotype, designated by Yeo [1992: 199], P!; isoelectotype, B destroyed, K!, LE). Figure 4.

Geranium strigosum var. *platylobum* Franch., Pl. Delavay.: 113. 1889. *Geranium platylobum* (Franch.) R. Knuth in Engl., Pflanzenr. IV. 129 (Heft 53): 183. 1912. TYPE: China. Yunnan: montis Che-tcho-tze, supra Tapin-tze, 25°34'N, 100°14'E, 6 Aug. 1887, *P. J. Delavay* 2756 (lectotype, designated by Kunth [1912: 183], P!; isoelectotype, K!).

Perennial herbs, 16–72 cm. Stem erect or ascending, leafy, with uncinat, eglandular hairs 0.1–0.3 mm, patent, eglandular hairs 0.5–3.3 mm (sometimes lacking), and patent, glandular hairs 0.3–3.5 mm. Basal leaves in a \pm persistent rosette, cauline leaves opposite; leaf laminae (2.4)3.5–4.4(5.3) \times 3.2–8.4 cm, palmatifid (ratio of main sinus length:middle segment length = [0.55]0.68–0.77[0.81]), polygonal in outline, base cordate, pilose, with \pm appressed, eglandular hairs and plane, glandular hairs on both surfaces; segments 5, middle segment obtriangular, 4.8–11.7 mm wide at base, 9- to 16-lobed in distal half; petioles up to 15 cm, with uncinat eglandular hairs 0.1–0.3 mm, patent, eglandular hairs 0.4–3.1 mm (sometimes lacking), and patent, glandular hairs 0.4–3.2 mm; stipules 3.9–13.2 \times 0.9–3.1 mm, lanceolate, free, green, with scattered eglandular hairs on abaxial surface and margin, glabrous adaxially. Inflorescence a dichasial cyme with monochasial branches; cymules 2-flowered, solitary; peduncles (11)69–129(145) mm, with uncinat, eglandular hairs 0.1–0.3 mm, patent, eglandular hairs 0.5–3.2 mm (sometimes lacking), and patent, glandular hairs 1.2–2.4 mm; bracteoles 4.5–6.6 \times 0.5–1.1 mm, lanceolate, whorled; pedicels (8.1)0.3–22(31.8) mm, with uncinat, retrorse eglandular hairs 0.1–0.3 mm, patent,

eglandular hairs 0.2–2.2 mm (sometimes lacking), and patent, glandular hairs 0.6–2 mm. Flowers actinomorphic. Sepals (4.9)5.2–6.4(7.3) \times 2.1–3 mm, lanceolate, smooth, not accrescent, with mucro 0.8–2.4 mm (ratio of mucro length:sepal length = 0.17–0.35), with \pm patent, eglandular hairs 0.1–0.5 mm and patent, glandular hairs 1–3.4 mm on abaxial surface, glabrous adaxially. Petals (8.6)9–9.8(10.6) \times 3.9–7.3 mm, erect-patent, entire, without claw, white to purple, hairy on base of adaxial surface, usually glabrous on abaxial surface, ciliate on basal margin. Staminal filaments 3.8–5.1 mm, lanceolate, white, pilose on abaxial surface, ciliate on proximal half, with hairs 0.2–0.9 mm; anthers 1.2–1.7 mm, unknown color. Nectaries 5, hemispheric, with a tuft of hairs at top, dorsally glabrous. Gynoecium 3.1–5.9 mm, pink. Fruit 23–28 mm; mericarps 3.7–4.7 \times 1.2–1.8 mm, reticulate, brown, with \pm appressed, eglandular hairs 0.1–0.2 mm; rostrum 16–20 mm, without narrowed apex or with narrowed apex 0.5–1 mm, with patent, eglandular hairs 0.1–0.2 mm and patent, scattered, glandular hairs 0.1–0.7 mm; stigmatic remnants 1.5–2.4 mm, with 5 glabrous lobes. Seeds 2.2–3.3 \times 1–1.5 mm, smooth, brown. Chromosome number not known.

Additional illustrations. Tan (1991: 35, tab. 9, fig. 7, sub *Geranium platylobum*; 37, tab. 10, figs. 1–3); Wu and Chen (1991: 86, tab. 25, figs. 1–2; 5, sub *G. platylobum*); Xu et al. (1998: 49, tab. 13, figs. 1–6, sub *G. platylobum*).

Phenology. *Geranium hispidissimum* has been collected in flower from May to November.

Distribution and habitat. *Geranium hispidissimum* is present in Sichuan and Yunnan Provinces in southwestern China, in meadows, among shrubs in open rocky slopes, and in forest edges of pines or of mixed deciduous broad-leaved evergreen and conifers. This species is found at altitudes of 2000–3200 m. Figure 5.

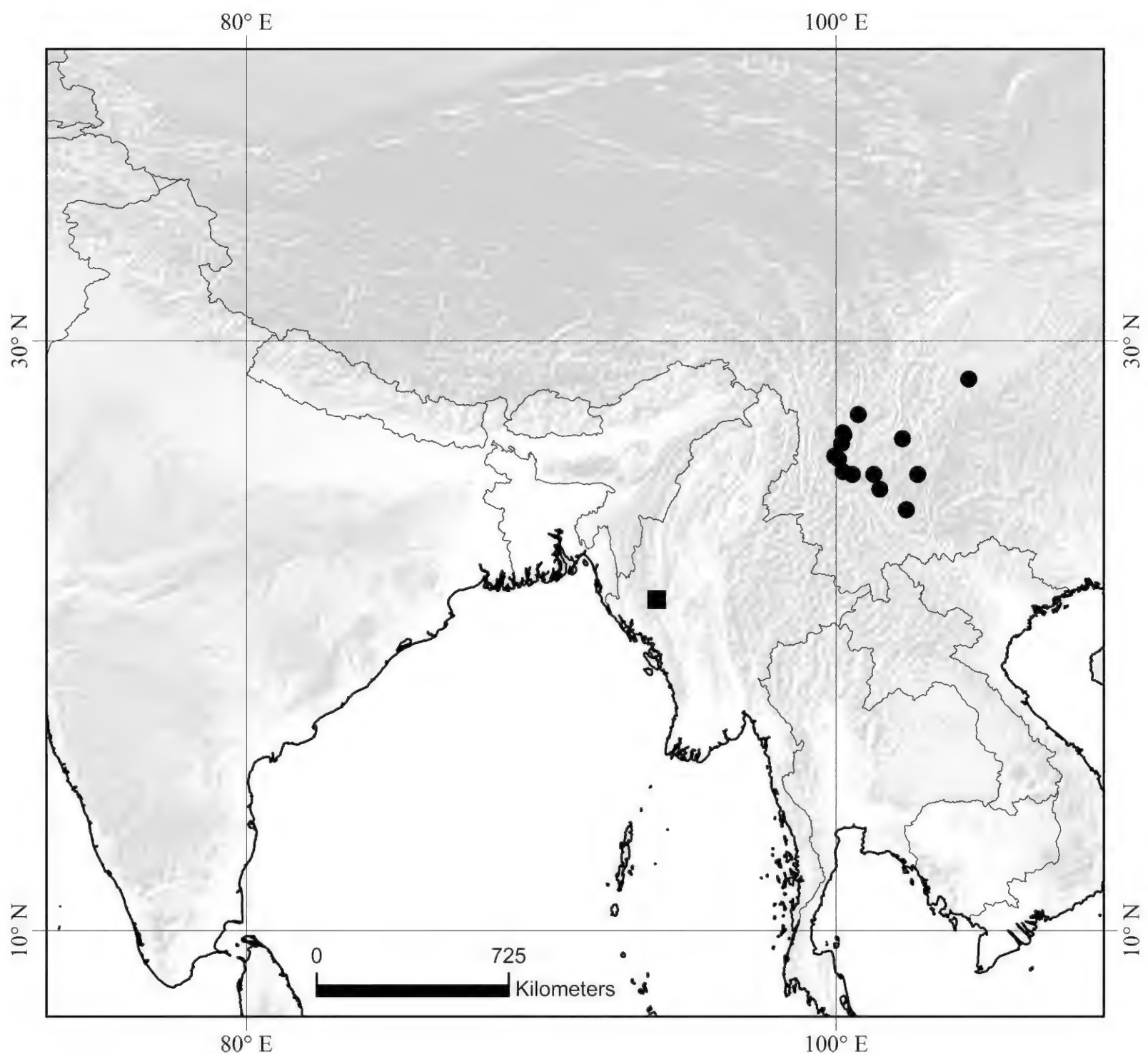


Figure 5. Distribution of *Geranium hispidissimum* (Franch.) R. Knuth (dots) and *G. wardii* Yeo (squares).

Discussion. *Geranium hispidissimum* shares with *G. strictipes* an erect habit, stout, vertical rootstock, opposite leaves, and inflorescence in dichasial cyme with monochasial branches. *Geranium hispidissimum* is, however, easy to identify from its less deeply divided leaves and its shorter petals. It also has shorter sepals, staminal filaments, anthers, fruit, rostrum narrowed apex and seeds. These features overlap to some degree. The indumentum of *G. hispidissimum* is also variable but is usually denser than in *G. strictipes*, especially on the leaves. *Geranium hispidissimum* and *G. strictipes* share with *G. moupinense* sepals with longer mucro. In these species the sepal mucro is green; in the remaining species of the section it is purple. The ranges of *G. hispidissimum* and *G. strigosum* overlap, and they occur sometimes in the same locality. Knuth (1912) recognized *G. platylobum* but did not indicate any

difference from *G. strictipes* to key it out. According to Yeo (1992), *G. platylobum* is an extreme case with unusual rounded leaf segments and obtuse lobes. The study of the type material shows that *G. platylobum* has short petals and leaves that are not as deeply divided as in *G. hispidissimum*.

Additional specimens examined. CHINA. **Sichuan:** Huei-li Hsien, 26°41'N, 102°15'E, *T. T. Yü* 1541 (CH). **Yunnan:** Yun-nan-sen, 25°28'N, 100°33'E, *Bélard* 15 (P); entre Yun-nan-sen et Nang-tzé, 25°28'N, 100°33', Aug. 1897, *Bélard s.n.* (P); Ahsi NW Likang-Snow range on Yangtze, 26°48'N, 100°16'E, *R. C. Ching* 20787 (A, PE); col du Hee-chan-men, 26°6'N, 99°57'E, *P. J. Delavay* 4827 (MA, P); Yunnan sen, 25°28'N, 100°33'E, *F. Ducloux* 432 (P); Chien Chuan to Sung Kwei pass, 25°59'N, 100°5'E, *G. Forrest* 132 (E); Yunnan, prope urbem Yungbei, inter vic. Dschaoping et Boloti, 24°16'N, 102°23'E, *H. F. Handel-Mazzetti* 3358 (W, WU); ad orientem urbis Lidjiang (Likang) supra vicum Duinaoko, 24°58'N, 101°29'E, *H. F. Handel-Mazzetti* 3461 (W, WU); near Ta-tsang-kai,

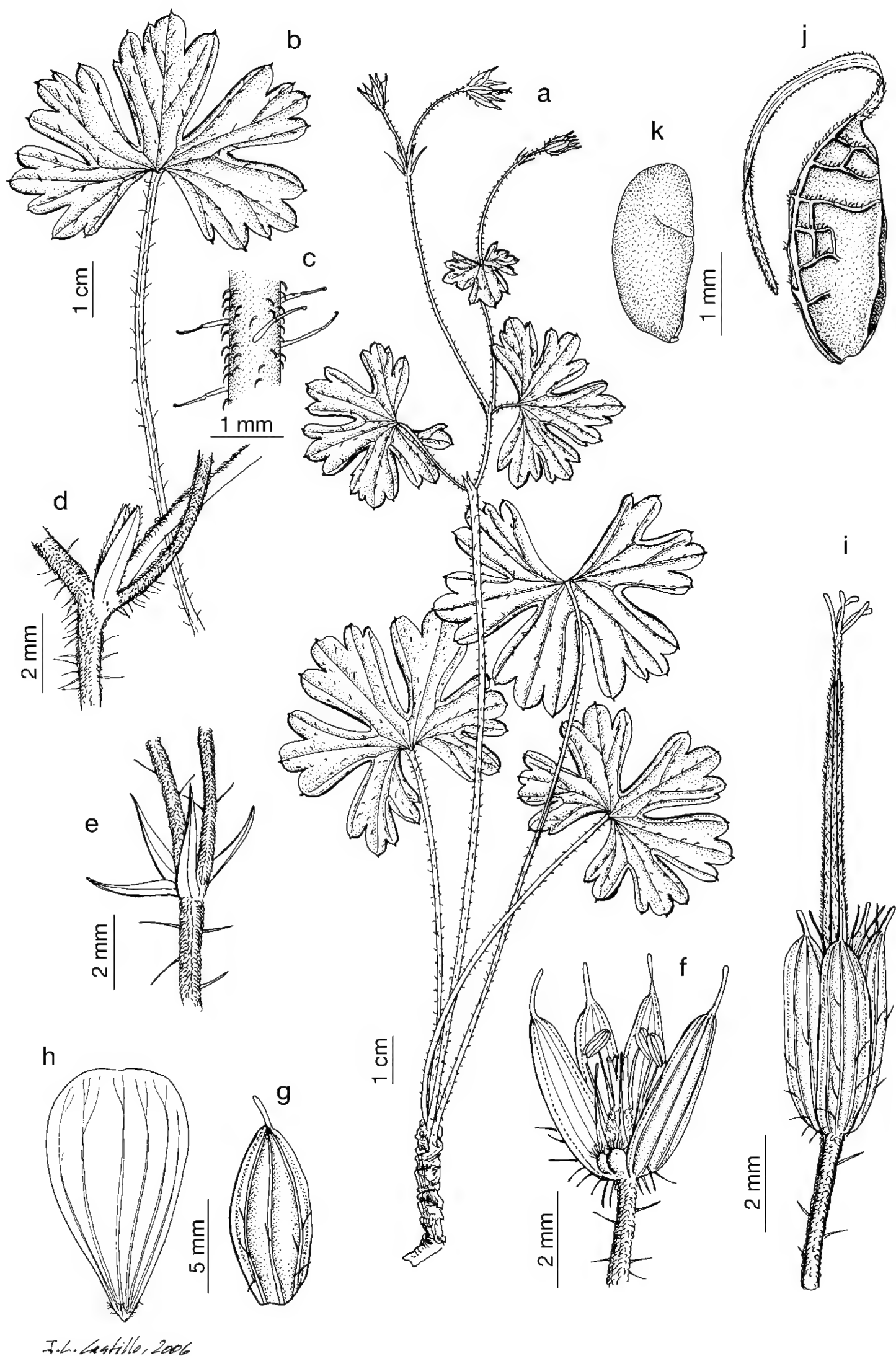


Figure 6. *Geranium moupinense* Franch. —A. Habit. —B. Leaf. —C. Petiole indumentum. —D. Stipules. —E. Bracteoles. —F. Flower without petals. —G. Sepal. —H. Petal. —I. Fruit. —J. Mericarp. —K. Seed. Based on A. David s.n. (MA-628480).

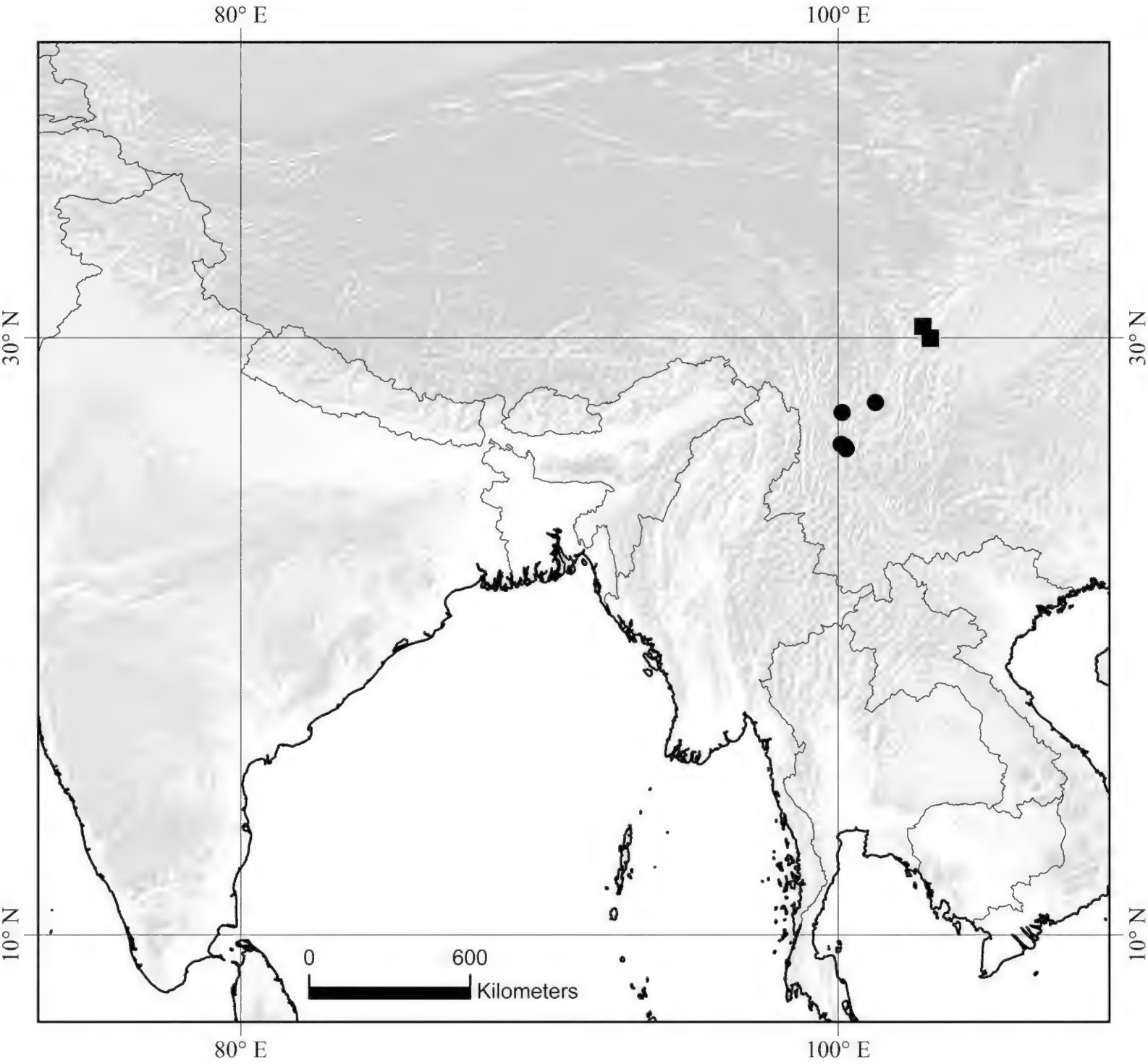


Figure 7. Distribution of *Geranium umbelliforme* Franch. (dots) and *G. moupinense* Franch. (squares).

27°30'N, 100°45'E, *F. Kingdon Ward 3971* (E); Yun-nan sen, 25°28'N, 100°33'E, *E. E. Maire 2577* (E); Yun-nan sen, 25°28'N, 100°33'E, *E. E. Maire 884* (BM); Ta Kai plateau, 1913, *E. E. Maire s.n.* (E); Lou Pou mtns., 25°28'N, 101°17'E, *E. E. Maire s.n.* (P); Dongchouan, 25°28'N, 101°17'E, July, *E. E. Maire s.n.* (BM, E, P); ad viam Yunnanfu-Suifu, 28°42'N, 104°30'E, 4 Sep. 1914, *R. Mell s.n.* (W); distr. Dali, población He Qing, montaña Ma Er Shan, 26°31'N, 100°11'E, *Qin 23372* (E, PE); Songmoing Xian, in the vic. of Longtan, 59 km N of Kunming, 25°28'N, 102°46'E, *Sino-Amer. Bot. Exped. 1349* (A, CAS, E, K); *C. W. Wang 70873* (A); Li-kiang Hsien, 26°53'N, 100°14'E, *C. W. Wang 71296* (A).

2. *Geranium moupinense* Franch., *Nouv. Arch. Mus. Hist. Nat.* ser. 2 8(2): 208. 1885. TYPE: China. Sichuan: Moupine, 30°23'N, 102°50'E, June 1869, *A. David s.n.* (lectotype, here designated, P!; isotype, MA!). Figure 6.

Geranium ascendens Z. M. Tan, *Bull. Bot. Res.*, Harbin 10(1): 23, tab. 1. 1990. TYPE: China. Sichuan: Yaan,

29°59'N, 103°05'E, 1988, *Chengdu College of Traditional Chinese Medicine Exped. 102* (holotype, SZ image!; the type was originally at CDCM).

Perennial herbs, 12–25 cm. Stem erect, leafy, with uncinat, eglandular hairs 0.1–0.3 mm and patent, glandular hairs 0.7–1.1 mm. Basal leaves in a ± persistent rosette, cauline leaves alternate; leaf laminas 3.6–5.8 × 4.6–5.5 cm, palmatifid (ratio of main sinus length:middle segment length = 0.76–0.81), polygonal in outline, base cordate, pilose, with ± appressed, eglandular hairs and plane, glandular hairs on both surfaces; segments 5, middle segment obtriangular, 3.7–6.9 mm wide at base, 3- to 7-lobed in distal half; petioles up to 12 cm, with uncinat eglandular hairs 0.1–0.2 mm and patent, glandular hairs 0.8–1.1 mm; stipules 4.9–5.1 × 1.5–1.6 mm, broadly lanceolate, free, brown, with scattered eglandular hairs on abaxial surface and margin,

glabrous adaxially. Inflorescence a monochasial cyme; cymules 2-flowered, solitary; peduncles 48–72 mm, with uncinata, retrorse, eglandular hairs 0.2–0.3 mm and patent, glandular hairs 0.8–1.6 mm; bracteoles $5\text{--}6.6 \times 1\text{--}1.2$ mm, lanceolate, whorled; pedicels 25–28 mm, with uncinata, retrorse, eglandular hairs 0.2–0.3 mm and patent, glandular hairs 0.7–1.1 mm. Flowers actinomorphic. Sepals $7.9\text{--}8.9 \times 1.8\text{--}4.3$ mm, lanceolate, smooth, not accrescent, with mucro 1.7–1.8 mm (ratio of mucro length:sepal length = 0.19–0.22), with \pm patent, eglandular hairs 0.1–0.3 mm and patent, glandular hairs 1.4–1.8 mm. Petals $12\text{--}12.2 \times 5.3\text{--}7.7$ mm, erect-patent, entire, without claw, purple, hairy on base of both surfaces and margin with hairs ca. 0.2 mm. Staminal filaments 2.7–4 mm, lanceolate, white, pilose on abaxial surface, ciliate on proximal half, with hairs 0.4–1 mm; anthers 1.6–1.7 mm, unknown color. Nectaries 5, hemispheric, with tuft of hairs at top, dorsally glabrous. Gynoecium 5–5.5 mm, unknown color. Fruit 20–23 mm; mericarps $3\text{--}3.2 \times 1\text{--}1.1$ mm, reticulate, brown, with \pm appressed, eglandular hairs 0.1–0.2 mm; rostrum 16.5 mm, with narrowed apex 1.5–1.7 mm, with patent, eglandular hairs 0.2–0.3 mm; stigmatic remnants 1.8–2 mm, with 5 glabrous lobes. Seeds $2\text{--}2.1 \times 0.9\text{--}1$ mm, smooth, brown. Chromosome number not known.

Additional illustrations. Xu et al. (1998: 51, tab. 14, fig. 7).

Phenology. *Geranium moupinense* has been collected in flower in June.

Distribution and habitat. *Geranium moupinense* is present in Sichuan Province, in southwestern China, in shaded areas at unknown altitudes. Figure 7.

Discussion. *Geranium moupinense* is an erect perennial herb that shares the feature of alternating leaves on the stem with *G. polyanthes* and *G. umbelliforme*. It is easily differentiated from these species by its solitary cymules (not in umbel-like aggregates) with well-developed peduncles and pedicels. *Geranium moupinense* also has noticeably longer sepals, mucro, and nectaries, with a tuft of hairs at the top (not glabrous). Additionally, the leaves of *G. moupinense* have fewer lobes per segment. The bracteoles, sepals, and anthers are longer, and the eglandular hairs on the inflorescence are shorter. These features overlap to some degree. *Geranium moupinense* shares with *G. umbelliforme* a fruit rostrum with a well-developed narrowed apex. Unfortunately, among the few available collections,

the fruits and underground parts are poorly represented. Thus, more collections may help to clarify the degree of character variation in both rootstock and fruits within this species.

Geranium moupinense is a rare species only known from three herbarium sheets, two at P and one at MA, which seems to be part of the same gathering. They bear a similar printed label with the date “1870.” According to Franchet (1885), the collection by A. David was made in June 1869. Other species from the “Plantae Davidianae” have the same inconsistency (e.g., *Meliosma cuneifolia* Franch. [P-00732482], with a printed label dated 1870). Fortunately, in some cases the original handwritten label was kept (e.g., *Deutzia longifolia* Franch. [P-00709448], which shows that 1869 was changed to 1870 on the printed label). Yeo (1992) studied the specimens at P but considered the type as “not located.” The present data strongly suggest that these specimens with only a printed label are original material, and consequently a lectotype is proposed here.

Yeo (1992) accepted *Geranium ascendens* in his treatment of Chinese geraniums, although he examined neither the type nor the other specimens. On the basis of the protologue he considered *G. ascendens* to be related to *G. moupinense* and *G. wardii* but only pointed out its differences in regard to the latter. Xu et al. (1998) and Xu and Aedo (2008) considered *G. ascendens* a synonym of *G. moupinense*. An image of the type of *G. ascendens* fits well with *G. moupinense* because of its alternate cauline leaves, leaf lamina not deeply divided, and solitary cymules. These reasons support retaining *G. ascendens* in the synonymy of *G. moupinense*, at least until new evidence appears.

3. *Geranium nakaoanum* H. Hara, Acta Phytotax. Geobot. 16: 1. 1954. TYPE: Nepal. Chaikia to Kalun, $28^{\circ}35'N$, $81^{\circ}37'E$, 2 July 1953, S. Nakao s.n. (holotype, KYO!). Figure 8.

Perennial herbs, 7–27 cm. Stem erect or ascending, leafy, glabrous. Basal leaves in a \pm persistent rosette, cauline leaves opposite (rarely alternate in middle of shoot, first node); leaf laminae $(1.2)1.6\text{--}2.2(2.5) \times 1.5\text{--}3.1$ cm, palmatifid (ratio of main sinus length:middle segment length = $[0.66]0.77\text{--}0.82[0.84]$), polygonal in outline, base cordate, pilose, with \pm appressed, eglandular hairs and plane, glandular hairs on adaxial surface and glabrous on abaxial surface; segments 5, middle segment obtriangular, 1.4–2.9 mm wide at base, 3- to 8-lobed in distal half; petioles up to 18 cm, usually glabrous, sometimes with scattered eglandular hairs

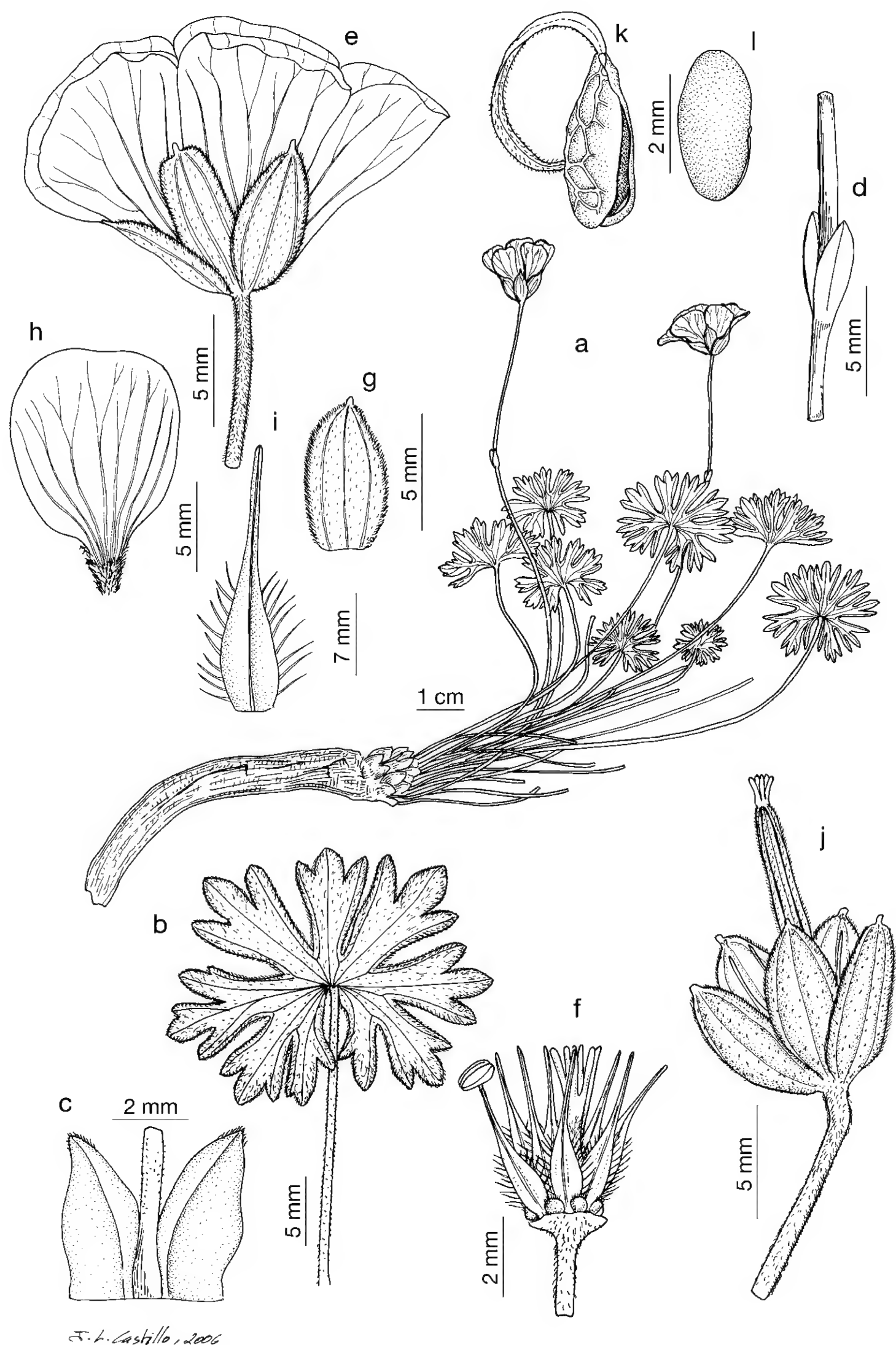


Figure 8. *Geranium nakaoanum* H. Hara. —A. Habit. —B. Leaf. —C. Stipules. —D. Bracteoles. —E. Flower. —F. Flower without petals and sepals. —G. Sepal. —H. Petal. —I. Staminal filament. —J. Fruit. —K. Mericarp. —L. Seed. A, B, D–F based on *S. Nakao* s.n. (KYO); C based on *D. McCosh* 354 (BM); G–I based on *J. D. Stainton* 7384 (BM); J–L based on *C. Wigram* 31 (K).

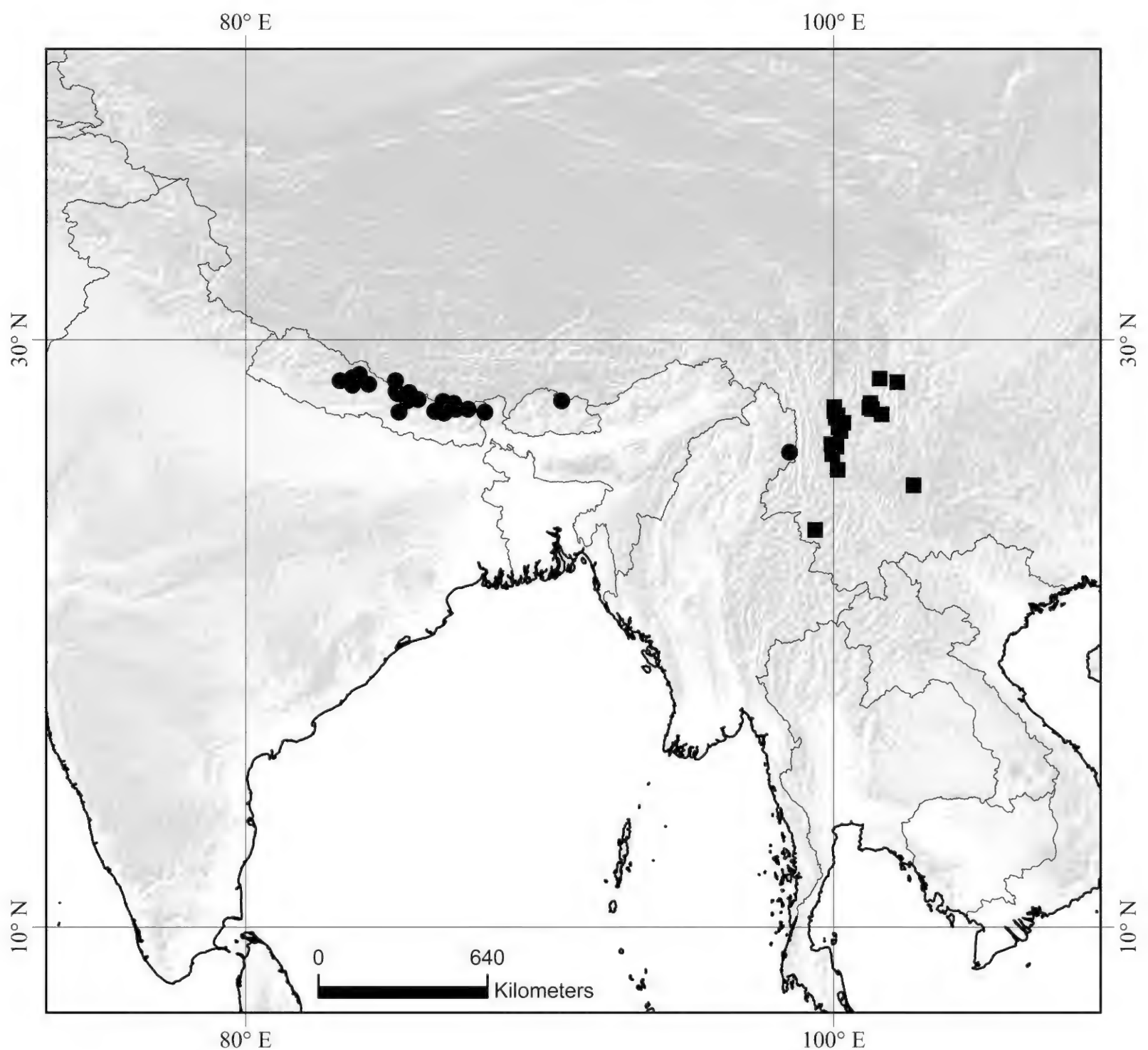


Figure 9. Distribution of *Geranium nakaoanum* H. Hara (dots) and *G. strictipes* R. Knuth (squares).

0.1–0.2 mm; stipules $2.9\text{--}4 \times 1.3\text{--}2$ mm, ovate, obtuse, free, brown, with scattered eglandular hairs on abaxial surface and margin, glabrous adaxially. Inflorescence a monochasial cyme; cymules 1(2)-flowered, solitary; peduncles 28–69(106) mm, with uncinat, retrorse, eglandular hairs 0.1–0.3 mm; bracteoles $2.7\text{--}4.9 \times 0.9\text{--}1.5$ mm, lanceolate, obtuse, subopposite; pedicels 21–44(65) mm, with uncinat, retrorse, eglandular hairs 0.2–0.3 mm. Flowers actinomorphic. Sepals (5.5)6.1–7(8.2) \times 2.6–3.3 mm, lanceolate, smooth, not accrescent, with mucro 0.4–0.6 mm (ratio of mucro length:sepal length = 0.07–0.11), with uncinat, antrorse, eglandular hairs 0.1–0.4 mm. Petals (11.5)13.1–15.9(16.1) \times 7–10.9 mm, erect-patent, entire, without claw, purple, hairy on base of adaxial surface, glabrous on abaxial surface, ciliate on basal margin with hairs 0.3–0.7 mm. Staminal filaments 3.5–4.6 mm, lanceolate with an abruptly narrowed apex, white, ciliate, with

eglandular hairs 0.3–1.4 mm; anthers 0.8–1 mm, yellow. Nectaries 5, hemispheric, glabrous. Gynoecium 3.7–4.3 mm, yellow. Fruit 14.5–22.9 mm; mericarps $4\text{--}4.3 \times 1.6\text{--}1.9$ mm, reticulate, brown, glabrous; rostrum 8.1–15.8 mm, without or with narrowed apex 0.5–0.8 mm, glabrous; stigmatic remnants 0.5–1.9 mm, with 5 glabrous lobes. Seeds $3\text{--}3.1 \times 1.3\text{--}1.4$ mm, smooth, brown. Chromosome number not known.

Additional illustration. Hara (1955: 277, fig. 83).

Phenology. *Geranium nakaoanum* has been collected in flower from February to August.

Distribution and habitat. *Geranium nakaoanum* is present in Himalaya, from central Nepal to Bhutan, plus in a locality in northern Burma. It is found in meadows, on open grassy or rocky slopes, and along trails, at altitudes of 3100–5000 m. Figure 9.

Discussion. *Geranium nakaoanum* is a small herb, with a vertical rootstock shortly branched at the apex and with short, erect, or ascending stems not rooting at the nodes. Basal leaves are arranged in a rosette, which is overtopped by the cymules. Cauline leaves are usually opposite, but in some individuals they are alternate in the middle of the shoot and opposite toward the apex. The cymules are borne on the short stem or, sometimes, on the rootstock. They are usually 1-flowered, although exceptionally some 2-flowered cymules occur in some predominantly 1-flowered individuals. The indumentum of the peduncles and pedicels consists of short, retrorsely appressed eglandular hairs. Both stems and petioles are glabrous, but some scattered, appressed, eglandular hairs were observed on the petioles of some individuals. Petals are long, with small hairs on the basal margin and on the base of the adaxial side. The staminal filaments have a distinctive narrowed apex and conspicuous ciliae. The variability of *G. nakaoanum* fruits should be checked with more fruiting material because only two mature fruits have been studied.

Geranium nakaoanum seems to be close to *G. polyanthes*, *G. umbelliforme*, and *G. moupinense* because of its monochasial inflorescence. It differs, however, from this group by its usually opposite leaves. *Geranium nakaoanum* shows singular characters in the section, e.g., its usually 1-flowered cymules, the scarce indumentum, and the staminal filaments with a narrowed apex.

According to Ikeda (pers. comm.), the description of *Geranium nakaoanum* was published in October 1954 (Hara, 1954) and later copied in *Flora and Fauna of Nepal* (Hara, 1955).

Additional specimens examined. BURMA. **Paijawnng Bum:** 26°10'N, 98°30'E, *F. Kingdon Ward 3438* (E). INDIA. **Bhutan:** Pangotang, Tsampa, 27°55'N, 90°45'E, *F. Ludlow & G. Sherrieff 19132* (BM, US). **Sikkim:** Bikbari campsite at the end of valley below HMI base camp, 27°32'N, 88°8'E, *B. N. Starling et al. 245* (K). NEPAL. Topke Gola, 27°38'N, 87°34'E, *L. W. Beer 8310* (BM); Maccherma, 27°54'N, 86°43'E, *J. F. Dobremez 360* (BM); Bhuanjene, 27°55'N, 85°30'E, *J. H. Haas 2118* (BM); C Nepal, Bagmati Zone, Rasuwa Distr., Gosain Kund–Bhairab Kund, 28°5'N, 85°25'E, *T. Hoshino et al. 9531084* (A); Bhairaukunda, 27°58'N, 85°52'E, *A. Maire 81* (E); Hongu Khola, 27°30'N, 86°45'E, *D. McCosh 354* (A, BM); E Nepal, Khosi Zone, Sankhuwa Sabha Distr., around Cha Ding Kharka, 27°40'N, 87°10'E, *M. Minaki et al. 90* (A, E); C Nepal, Bagmati Zone, Rasuwa Distr., around Jaisuli Kund, 28°11'N, 85°11'E, *F. Miyamoto et al. 9410140* (E); C Nepal, Bagmati Zone, Rasuwa Distr., Pabil Kharka-pass-Kharka, near Seto Kund, 28°15'N, 85°7'E, *F. Miyamoto et al. 9410228* (A, E); E Nepal, Sagarmatha Zone, Solukhumbu Distr., Gnaula-Pike, 27°33'N, 86°27'E, *F. Miyamoto et al. 9580047* (A); E Nepal, Khosi Zone, Sankhuwa Sabha Distr., Sano Birke–Jaggu Danda, 27°38'N, 87°9'E, S.

Noshiro et al. 9760340 (A); Langsisa Kharka, 28°12'N, 85°34'E, *O. Polunin 414* (BM); Dobhan, 27°32'N, 85°13'E, *K. N. Sharma E439* (BM); Mukinath, 28°49'N, 83°52'E, *J. D. Stainton et al. 1454* (A, BM, E); Taglung, S of Tukucha, Kali Gandaki, 28°42'N, 83°38'E, *J. D. Stainton et al. 1782* (BM); NW of Gurjakhani, 28°36'N, 83°13'E, *J. D. Stainton et al. 3101* (A, BM, E); Rambong, Lamjung Himal, 28°29'N, 84°11'E, *J. D. Stainton et al. 5991* (BM); Mailey Khiba, Central Nepal, 28°27'N, 83°38'E, *J. D. Stainton 7384* (BM); E Nepal, Khosi Zone, Sankhuwa Sabha Distr., around Makalu Base Camp, 27°50'N, 87°5'E, *M. Suzuki et al. 8820875* (A, E); E Nepal, Khosi Zone, Sankhuwa Sabha Distr., Cha Ding Kharka–Tutu La–Thulo Pokhari–Shipton Pass–Khongma, 27°40'N, 87°10'E, *M. Suzuki et al. 8821951* (E); E Nepal, Sagarmatha Zone, Solukhumbu Distr., Sete–Lamjura La–Taktor, 27°34'N, 86°26'E, *M. Wakabayashi et al. 9720053* (A); E Nepal, Sagarmatha Zone, Solukhumbu Distr., Chalem Kharka–Panch Pokhari–Khola Kharka, 27°35'N, 86°50'E, *M. Wakabayashi et al. 9730142* (A); E Nepal, Sagarmatha Zone, Solukhumbu Distr., Khola Kharka–Rangdu Kharka, 27°36'N, 86°50'E, *M. Wakabayashi et al. 9730163* (A); Nepal, 11 Feb. 1924, *C. Wigram s.n.* (K); Ganesh Himal, 28°10'N, 85°10'E, *B. Yon 192* (E).

4. *Geranium polyanthes* Edgew. & Hook. f. in Hook. f., *Fl. Brit. India* 1: 431. 1874. TYPE: India. Uttaranchal: Kumaon, 29°24'N, 79°30'E, *R. Blinkworth 8564* (lectotype, designated by Yeo [1992: 192], K!; isolectotypes, P!, W!). Figure 10.

Perennial herbs, 7–64 cm. Stem erect, leafy, subglabrous or with a variable indumentum composed by uncinat, eglandular hairs 0.1–0.3 mm, and sometimes patent, eglandular hairs 0.8–2.2 mm and patent, glandular hairs 0.2–1.3 mm. Basal leaves in a \pm persistent rosette, cauline leaves alternate in middle of shoot and opposite at apex; leaf laminae (1.9)2.8–4.9(5.6) \times 2.7–6.5 cm, palmatifid (ratio main of sinus length:middle segment length = [0.61]0.71–0.76[0.81]), polygonal in outline, base cordate, pilose, with \pm appressed, eglandular hairs and plane, glandular hairs on both surfaces; segments 5, middle segment obtriangular, 3.4–8.9 mm wide at base, 3- to 10-lobed in distal half; petioles up to 32 cm, subglabrous or with variable indumentum composed by uncinat eglandular hairs 0.1–0.3 mm, and sometimes patent, eglandular hairs 0.4–1.9 mm and patent, glandular hairs 0.5–1.2 mm; stipules 4.9–8.3 \times 1.5–4.8 mm, ovate, obtuse, free, brown, with scattered eglandular hairs on abaxial surface and margin, glabrous adaxially. Inflorescence a monochasial cyme; cymules 2(3)-flowered, in dense umbel-like aggregates at top of each branch; peduncles 0(73) mm, with patent, eglandular hairs 0.6–0.7 mm; bracteoles 2.3–5.6 \times 0.5–1.6 mm, lanceolate, obtuse, whorled; pedicels (1.9)3.2–17(25) mm, with uncinat, re-

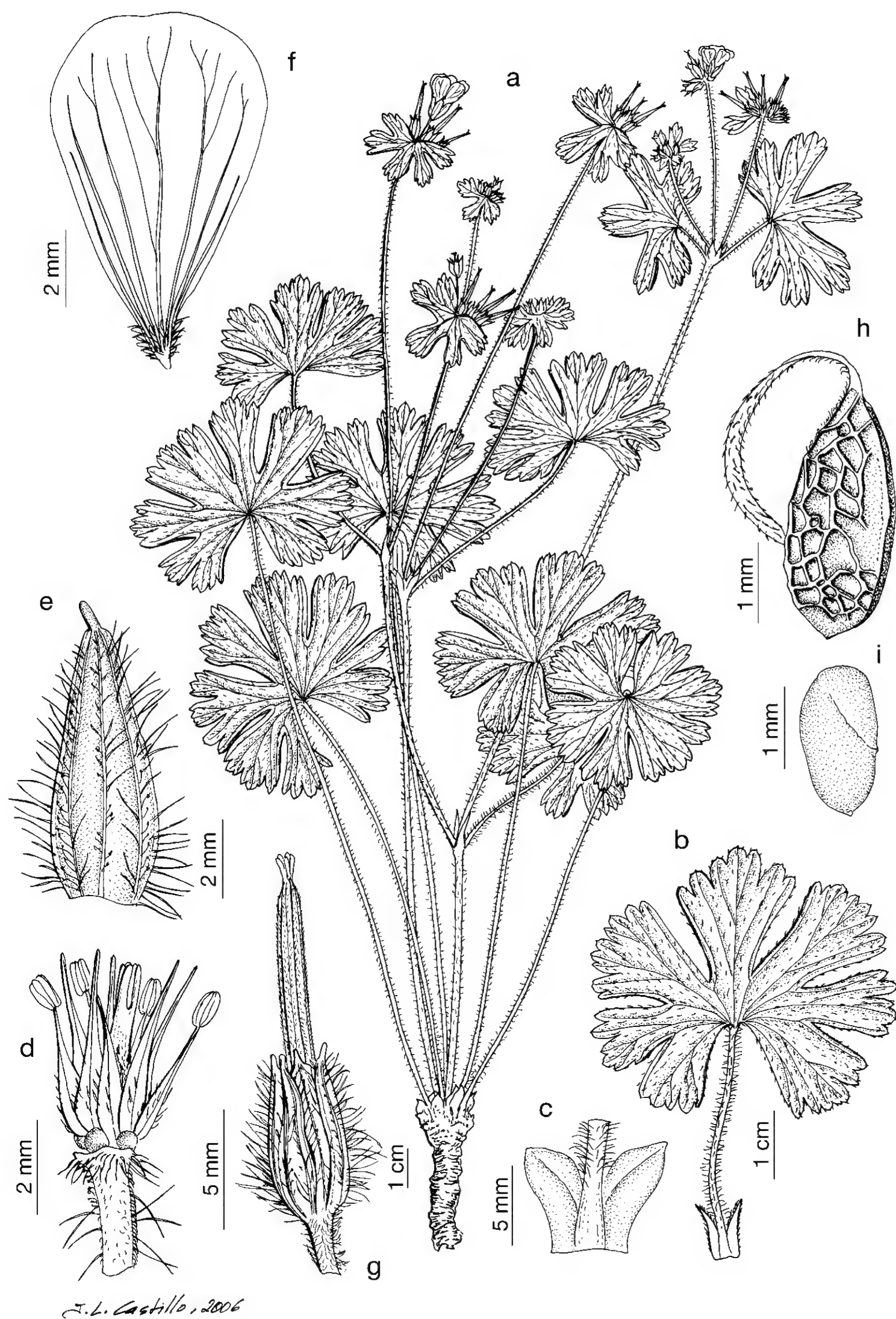


Figure 10. *Geranium polyanthes* Edgew. & Hook. f. —A. Habit. —B. Leaf. —C. Stipules. —D. Flower without petals and sepals. —E. Sepal. —F. Petal. —G. Fruit. —H. Mericarp. —I. Seed. A, C–I based on *F. Ludlow et al.* 5225 (BM); B based on *T. T. Yü s.n.* (KUN-280350).

trorse, eglandular hairs 0.2–0.3 mm, patent, eglandular hairs 1–2.3 mm, and usually, patent, glandular hairs 0.4–0.7 mm. Flowers actinomorphic. Sepals (4.9)5.7–6.9(8.2) \times 1.7–3.9 mm, lanceolate, smooth, not accrescent, with mucro 0.4–0.9 mm (ratio of mucro length:sepal length = 0.06–0.16), with \pm patent, eglandular hairs 0.2–2.6 mm and patent, glandular hairs 0.4–1.1 mm on abaxial surface, glabrous adaxially. Petals (7.8)9.3–11.8(14.1) \times 5.1–9.1 mm, erect-patent, entire or retuse, without claw, purple, hairy on base of adaxial surface, glabrous on abaxial surface, ciliate on basal margin with hairs 0.4–0.7 mm. Staminal filaments 2.6–4.6 mm, lanceolate, white, pilose on abaxial surface, ciliate on proximal half, with hairs 0.3–0.7 mm; anthers 0.6–1.1 mm, yellow. Nectaries 5, hemispheric, glabrous. Gynoecium 3.2–4.9 mm, pink. Fruit 13–21.7 mm; mericarps 3.1–4.7 \times 1.2–1.7 mm, reticulate, brown, with \pm appressed, eglandular hairs 0.1–0.2 mm; rostrum 9.2–16.3 mm, without narrowed apex or with narrowed apex 0.5–1 mm, with patent, eglandular hairs 0.2–0.5 mm, and sometimes scattered, patent, glandular hairs 0.2–0.3 mm; stigmatic remnants 0.7–1.7 mm, with 5 glabrous lobes. Seeds 1.9–2.8 \times 0.9–1.4 mm, smooth, brown. Chromosome number: $2n = 28$ (Warburg, 1938: 468).

Additional illustrations. Wu and Chen (1991: 94, tab. 28, figs. 6–7); Xu et al. (1998: 51, tab. 14, figs. 1–6).

Phenology. *Geranium polyanthes* has been collected in flower from April to September.

Distribution and habitat. *Geranium polyanthes* is present in Himalaya, from Uttaranchal in North India to Yunnan in southwestern China, in alpine meadows, moist fields, grassy slopes, damp banks, amongst boulders, and on the edges of *Abies* Mill., *Juniperus* L., *Picea* A. Dietr., or *Rhododendron* L. forests. The species is found at altitudes of 2000–4600 m. Figure 11.

Discussion. *Geranium polyanthes* is an erect perennial herb with a more or less vertical rootstock with thickened roots, leaves alternate in the middle of the shoot and opposite at the apex, and with a monochasial inflorescence. It is easy to identify by its distinctive dense aggregate of cymules at the apex of each branch. The cymules usually lack peduncles, have short pedicels, and are subtended by sessile or short petiolate leaves. Exceptionally, some solitary, peduncled cymules occur in individuals with cymules predominantly in umbel-like aggregates. Stipules are

ovate, obtuse, and conspicuously wide. *Geranium polyanthes* is close to *G. umbelliforme*, since both share a similar inflorescence structure and alternate cauline leaves. Nonetheless, *G. umbelliforme* has cymules in loose umbel-like aggregates usually with well-developed peduncles and narrower stipules.

According to Yeo (2002), some of the flowers of *Geranium polyanthes* are cleistogamous.

Additional specimens examined. BURMA. **Seinghku Wang:** 28°3'N, 97°35'E, *F. Kingdon Ward 7013* (K), 7221 (K). CHINA. **Xizang:** distr. Milin, 29°15'N, 93°0'E, *Exp. Medicina Herbacea China 3923* (PE); Tha Chu valley, 31°3'N, 81°19'E, *F. Kingdon Ward 19651* (BM); valley of the Di Chu, 28°20'N, 97°2'E, *F. Kingdon Ward 7194* (K); distr. Nie La Mu, pueblo Quxiang, 28°4'N, 85°59'E, *Liao Lian Rong 1911* (PE); Lo La Chu, near Molo, 28°55'N, 93°55'E, *F. Ludlow & G. Sherriff 1867* (BM); Tsari, 28°42'N, 93°18'E, *F. Ludlow & G. Sherriff 2124* (BM); Senguti, Tsari, 28°40'N, 93°20'E, *F. Ludlow & G. Sherriff 2467* (BM); Tamnyen Chu, Kongbo valley, 29°20'N, 94°43'E, *F. Ludlow & G. Sherriff 4899* (BM); Kongbo, SE Tibet, 29°30'N, 94°53'E, *F. Ludlow & G. Sherriff 14389* (BM); Kongbo, Doshong La, 29°31'N, 94°51'E, *F. Ludlow et al. 5225* (A, BM); Langong, 28°45'N, 94°0'E, *F. Ludlow & G. Sherriff 5504* (BM); distr. Motuo, pueblo Nage, 28°44'N, 94°53'E, *Qinghai-Tibet Exp. 74-3802* (PE); Thibet oriental, Sila Kynadla, 28°29'N, 98°54'E, *J. A. Soulié 1099A* (P); Thibet oriental, Sila Thrhana, 28°29'N, 98°54'E, *J. A. Soulié 1312A* (P); upper Kiubiang Valley, Chulung, Chialohmuto, 28°18'N, 89°12'E, *T. T. Yü 19713* (A, E, KUN); upper Kiubiang Valley, Chulung, Chialohmuto to Tsugum Mtn., 28°18'N, 89°12'E, *T. T. Yü s.n.* (KUN). **Yunnan:** Tsekou, 28°29'N, 98°54'E, June 1905, *A. K. Bulley s.n.* (K); distr. Deqin, rivera del río Cangjiang, montaña Yongzi, 28°29'N, 98°54'E, *K. M. Feng 6449* (PE); distr. Deqin, rivera del río Cangjiang, montaña Yongzi, 28°29'N, 98°54'E, *K. M. Feng 6521* (PE); Lancang/Jinsha Jiang divide, Awa, 27°25'N, 99°18'E, *G. Forrest 25537* (E, NY, P, W); Gongshan Xian, Cikai Zheng, Labadi, along a branch of the Pula He on the rd. from Gongshan to Kongdang, E side of Gaoligong Shan, 27°48'N, 98°29'E, *Gaoligong Shan Biodiversity Survey 16972* (CAS, GH); Gongshan, Cikai, ca. 1.2 km SSE of the Heipa Pass tunnel on the new rd. from Gongshan to the Dulong Jiang valley, 27°45'N, 98°27'E, *Gaoligong Shan Biodiversity Survey 32158* (CAS); Gongshan, Cikai, near Yipsaka lake, 2.1 km SSE of Heipa Pass tunnel on the new rd. from Gongshan to the Dulong Jiang valley, E side of Gaoligong Shan, 27°45'N, 98°27'E, *Gaoligong Shan Biodiversity Survey 32220* (CAS, GH, MA); Gongshan, Bingzhongluo, SW of Fucui, betw. Niwalo & Chukuai lake along N side of Nianwaluo He, 12.4 km WSW of Bingzhongluo, E side of Gaoligong Shan, 27°59'N, 98°30'E, *Gaoligong Shan Biodiversity Survey 32907* (CAS, GH, MA); jugi Schöndsu-la inter fluvios Lu-djiang (Salween) et Landsang-djiang (Mekong), 28°4'N, 98°44'E, *H. F. Handel-Mazzetti 8253* (WU); inter fluvios Lu-djiang (Salween) et Djiou-djianj (Irradi Orient.), 27°58'N, 98°50'E, *H. F. Handel-Mazzetti 9525* (W, WU); sources of the Irrawaddy, Adung valley, 28°20'N, 97°40'E, *F. Kingdon Ward 9783* (BM); Tsekou, 28°29'N, 98°54'E, June 1905, *T. Manberg s.n.* (K); Mt. Kenyichunpo & region of Champutong, Salween-Irrawadi watershed, 28°3'N, 98°35'E, *J. F. Rock 10188* (E, US); Si-Kang, Chi-na-tung, Tsawa-rung, 27°45'N, 98°42'E, *C. W. Wang 65221* (A);

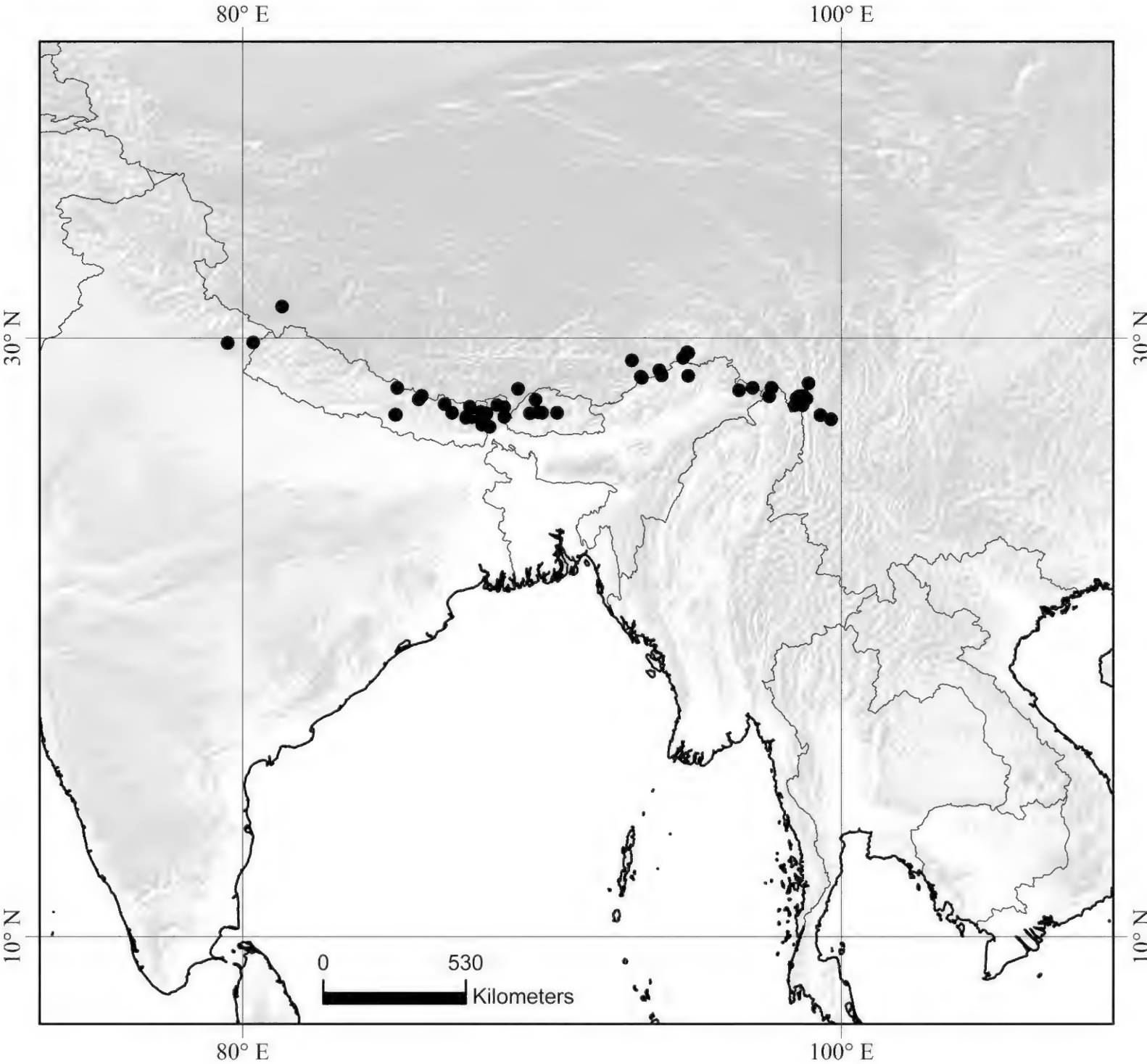


Figure 11. Distribution of *Geranium polyanthes* Edgew. & Hook. f.

Upper Kiukiang Valley (Clulung), Chialahmuto, 27°17'N, 99°39'E, *T. T. Yü* 19713 (GH); Mekong-Salween, Sewalongba, 28°4'N, 98°44'E, *T. T. Yü* 22528 (A, E). **INDIA.** **Assam:** Dolei valley, 28°15'N, 96°35'E, *F. Kingdon Ward* 8667 (K). **Bhutan:** Tsonga, 27°30'N, 90°30'E, *R. E. Cooper* 2286 (E); Phajudin [Pajoding] Juipu, 27°31'N, 89°52'E, *R. E. Cooper* 2548 (E); Nabi to Hinglai-La, 27°30'N, 90°0'E, *B. J. Gould* 844 (K); above Motithang, Thimphu, 27°29'N, 89°36'E, *A. J. Grierson & D. G. Long* 2742 (E); Upper Mo Chu Distr., betw. Gasa & Pari La, 27°56'N, 89°47'E, *I. W. Sinclair & D. G. Long* 5052 (E). **Sikkim:** Sikkim, Tongloo, *T. Anderson* 412 (M); Sikkim, 27°45'N, 88°30'E, *G. H. Cave* 30 (WRSL); Eantso La, 27°45'N, 88°30'E, *G. H. Cave* 1212 (WRSL); Yampung, 27°23'N, 88°5'E, 1 July 1922, *G. H. Cave s.n.* (E); Jolumbo, 27°45'N, 88°30'E, *C. B. Clarke* 25608 (K); Kapup, 27°22'N, 88°44'E, *R. E. Cooper* 761 (E); Sikkim, Lachung valley, 27°41'N, 88°44'E, Aug. 1892, *G. A. Gammie s.n.* (P, US, W); Damphibkei, 27°16'N, 88°2'E, *R. Lepcha & Ribu* 1088 (E); Jongri, 27°28'N, 88°9'E, 1913, *R. Lepcha & Ribu* 6590 (E); West Distr., Chhurong, Chhu valley betw. Jamlinghang & Bikbari, 27°29'N, 88°9'E, *D. G. Long et al.* 238 (E); West Distr., Dzongri, 27°28'N,

88°9'E, *D. G. Long et al.* 427 (E); apud vicum Yumthang, 27°41'N, 88°44'E, 16 Aug. 2003, *M. Nohelová s.n.* (B). **Uttaranchal:** Kumaon, Jimba, on way from Bonato to Darma Vy, 29°51'N, 80°21'E, *W. Koelz* 20970 (NY). **West Bengal:** Darjiiling, 27°2'N, 88°15'E, *C. B. Clarke* 27598 (K); Singalila Ridge, Sandakphu, 27°6'N, 88°0'E, *G. Rai* 312 (B). **NEPAL.** Iswa Khola, 27°30'N, 87°0'E, *L. W. Beer* 25495 (BM); Milke Dobaye, 27°23'N, 87°29'E, *J. F. Dobremez* 1582 (BM, E); Topke Gola, 27°42'N, 87°35'E, *J. F. Dobremez* 1722 (E); Taplejung, Ghunsa, Yonpma Khola valley above Phole, 27°21'N, 87°40'E, *Gray* 31 (K); Mechi Zone, Taplejung Distr., Lamo Pokhari–Dobate–Hike Khar-ka, 27°20'N, 87°28'E, *Y. Omori et al.* 9920037 (E); Mahalangur Himal, Khumbu, Paugpoche, 27°47'N, 86°45'E, *J. Poelt* 6329 (M); Chuwar, 27°26'N, 85°6'E, 14 *K. N. Sharma* 421 (E); Jshade, Ghopte, 27°26'N, 85°7'E, *T. B. Shrestha & P. R. Shakya* 3758 (US); Central Region, Bagmati Zone, Sindhupalchok Distr., Phunboche Danda, S Bhairab Kund, 27°57'N, 85°53'E, *M. F. Watson et al.* EKSIN 219 (E); Yimbua Yuola, 27°32'N, 87°57'E, *L. H. Williams* 824 (BM); Ganesh Himal, 28°20'N, 85°10'E, *B. Yon* 426 (E).

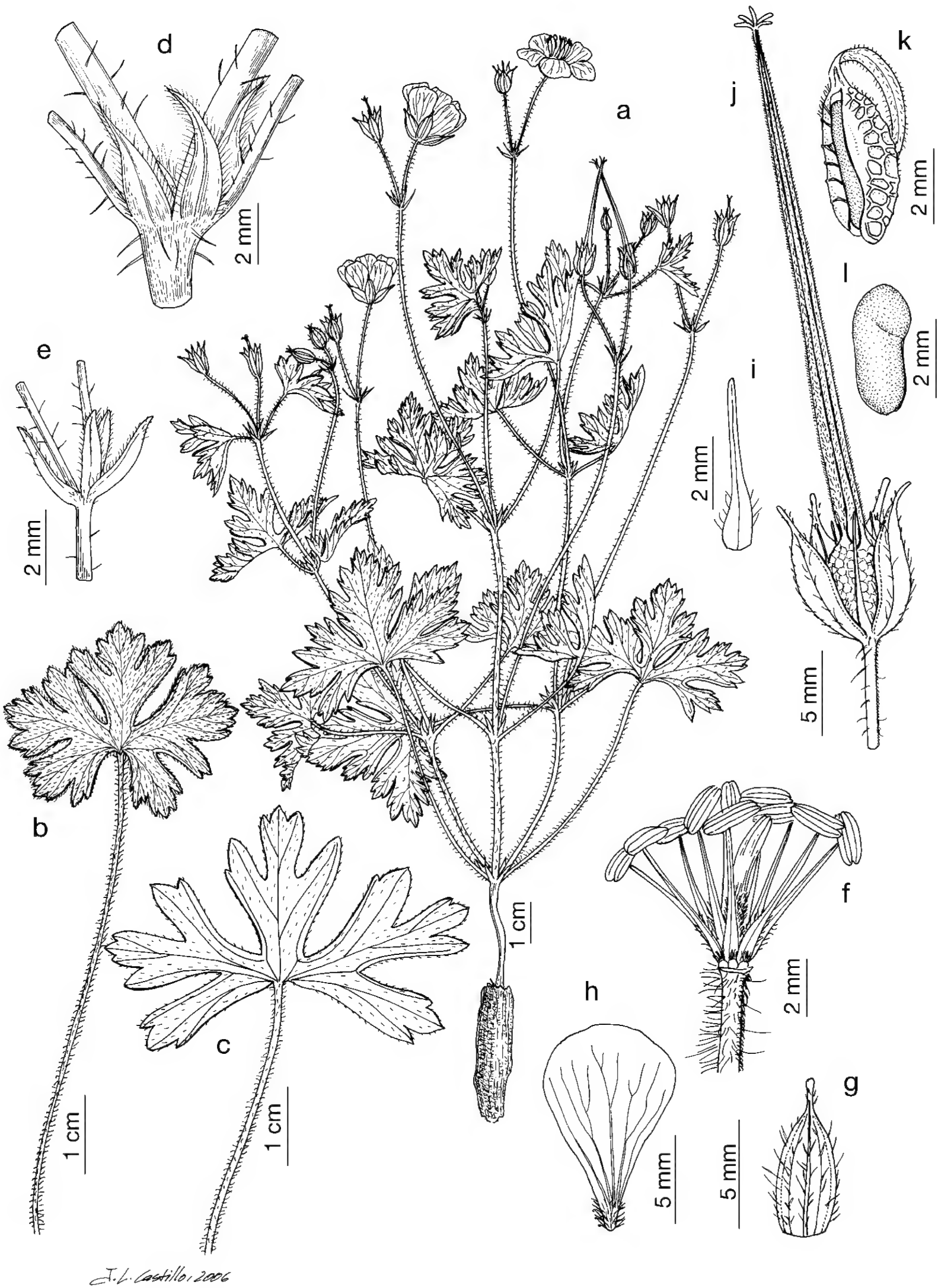


Figure 12. *Geranium strictipes* R. Knuth. —A. Habit. —B, C. Leaves. —D. Stipules. —E. Bracteoles. —F. Flower without petals and sepals. —G. Sepal. —H. Petal. —I. Staminal filament. —J. Fruit. —K. Mericarp. —L. Seed. A, C–I based on *G. Forrest* 2369 (BM); B based on *Zhong Dian Expedition* 606 (PE); J–L based on *G. Forrest* 6113 (E).

5. *Geranium strictipes* R. Knuth in Engl., Pflanzenr. IV. 129 (Heft 53): 581. 1912. TYPE: China. Yunnan: eastern flank of the Lichiang range, 27°20'N, 100°08'E, June 1906, *G. Forrest* 2369 (holotype, E!; isotypes, BM!, K!, P!). Figure 12.

Geranium strigosum Franch., Bull. Soc. Bot. France 33: 442. 1887, nom. illeg., non Burm. f., 1768. *Geranium strigosum* var. *gracile* Franch., Pl. Delavay. 113. 1889 (Yeo [1992: 197] designated the type of *Geranium strigosum* var. *gracile*; for more details see discussion). TYPE: China. Yunnan: montis Pe-ngay-tze, supra Houang-kia-pin, 25°34'N, 100°08'E, 4 Sep. 1882, *P. J. Delavay* *Geranium*, n. 2 (lectotype, designated here, P!).

Geranium strigosum var. *grandiflorum* Franch., Pl. Delavay. 113. 1889. *Geranium strictipes* var. *grandiflorum* (Franch.) C. Y. Wu ex H. W. Li, Vasc. Pl. Hengduan Mount. 1: 1026. 1993. TYPE: China. Yunnan: collum Koua-la-po, Hee-chan-men, 26°06'N, 99°57'E, 14 June 1887, *P. J. Delavay* s.n. (lectotype, designated here, P!; isoelectotypes, K!, NY!).

Perennial herbs, 20–76 cm. Stem erect or ascending, leafy, with patent, eglandular hairs 0.2–2.2 mm, and usually patent, glandular hairs 0.4–3.4 mm, sometimes subglabrous. Basal leaves in deciduous rosette, cauline leaves opposite; leaf laminae (1.8)2.5–3.6(4.9) × 2.8–5.9 cm, palmatifid (ratio of main sinus length:middle segment length = [0.70]0.80–0.86[0.89]), polygonal in outline, base cordate, pilose, with ± appressed, eglandular hairs and plane, glandular hairs on both surfaces; segments 5, middle segment rhombic, 3.2–10.6 mm wide at base, 8- to 16-lobed in distal half; petioles up to 15 cm, with uncinat, eglandular hairs 0.1–0.3 mm, patent, eglandular hairs 0.4–2 mm and usually patent, glandular hairs 0.2–2.7 mm; stipules 3.8–10 × 0.5–2.3 mm, lanceolate, free, green, with scattered eglandular hairs on abaxial surface and margin, glabrous adaxially. Inflorescence a dichasial cyme with monochasial branches; cymules 2-flowered, solitary; peduncles (40)51–82(109) mm, with uncinat, eglandular hairs 0.1–0.3 mm, patent, eglandular hairs 0.3–2.3 mm, and patent, glandular hairs 0.4–1.7 mm; bracteoles 3.1–8.9 × 0.4–1.2 mm, lanceolate, whorled; pedicels (4.6)9.7–21.9(25) mm, with uncinat, retrorse, eglandular hairs 0.2–0.3 mm, patent, eglandular hairs 0.2–1.9 mm, and patent, glandular hairs 0.4–1.7 mm. Flowers actinomorphic. Sepals (5.5)6.1–7.3(7.8) × 2.2–3.3 mm, lanceolate, smooth, not accrescent, with mucro 0.8–2.3 mm (ratio of mucro length:sepal length = 0.12–0.35), with patent, eglandular hairs 0.2–1.9 mm and patent, glandular hairs 0.8–2.8 mm on abaxial surface, glabrous adaxially. Petals (10.2)12–13.2(14.9) × 4.1–10.1 mm, erect-patent, entire or slightly notched (notch 0.5–1 mm deep), without

claw, purple, hairy on base of both surfaces and basal margin, with hairs 0.3–1 mm. Staminal filaments 3.7–6.2 mm, lanceolate, yellow, pilose on abaxial surface, ciliate on proximal half, with hairs 0.2–0.8 mm; anthers 1–2.7 mm, yellow. Nectaries 5, hemispheric, with a tuft of hairs at top, dorsally glabrous. Gynoecium 4.8–6.6 mm, yellow. Fruit 26–46.2 mm; mericarps 5–5.6 × 1.1–2.4 mm, reticulate, brown, with ± appressed, eglandular hairs 0.1–0.2 mm; rostrum 19–37 mm, with narrowed apex 1–2.6 mm, with patent, eglandular hairs 0.1–0.4 mm, and sometimes scattered, patent, glandular hairs 0.1–0.4 mm; stigmatic remnants 1.9–2.7 mm, with 5 glabrous lobes. Seeds 3.3–4.4 × 1.3–1.9 mm, smooth, brown. Chromosome number not known.

Additional illustrations. Tan (1991: 35, tab. 9, figs 1–6; 37, tab. 10, figs. 4–6, sub *Geranium strigosum*); Wu and Chen (1991: 86, tab. 25, figs. 3–4); Xu et al. (1998: 49, tab. 13, figs. 7–10).

Phenology. *Geranium strictipes* has been collected in flower from April to November.

Distribution and habitat. *Geranium strictipes* is present in Sichuan and Yunnan Provinces in southwestern China, in meadows, amongst scrub, and on stony banks at the edges of *Quercus* L. or *Pinus* L. forests. The species is found at altitudes of 1620–3660 m. Figure 9.

Discussion. *Geranium strictipes* is an erect herb with a very stout, more or less vertical rootstock, opposite leaves, and inflorescence a dichasial cyme with monochasial branches. According to Yeo (1992), *G. strictipes* is apparently the closest relative of *G. hispidissimum*. Their leaves, however, differ significantly. Leaves of *G. strictipes* are more deeply divided because the main and second sinuses are deeper. In addition, the main segment is narrower at the base in *G. strictipes*. The middle segment of the leaf lamina is rhombic in *G. strictipes*; in *G. hispidissimum* the middle segment is obtriangular. *Geranium strictipes* has longer petals, with more dense indumentum on the abaxial base, than in *G. hispidissimum*.

The indumentum of *Geranium strictipes* varies, with some individuals subglabrous on stem and petioles, to others covered by a quite dense indumentum. The glandular hairs are sometimes absent on the stem and the petioles and vary greatly in density on the inflorescence. According to Yeo (1992), the glandular hairs of *G. strictipes* have distinctly small swollen heads, while in *G. hispidissimum* they have minute terminal cells, occasionally swollen but usually not.

This feature seems to be constant in *G. strictipes* but varies in *G. hispidissimum*. In the latter, both glandular hairs with a minute or distinct head appear, which limits its taxonomic use.

Franchet (1887: 442) described *Geranium strigosum* as a species without infraspecific taxa from “Yun-nan, in dumetis Pe-ngay-tze, supra Houang-kia-pin; fl. fr. 4 sept. (Delav. n.).” Two years later Franchet (1889) recognized under his *G. strigosum* four varieties: α *hispidissimum*, β *grandiflorum*, γ *gracile*, and δ *platylobum*. Two of these are currently separated as *G. hispidissimum* (varieties α and δ) (Yeo, 1992). Neither of the remaining two have the epithet “*strigosum*,” which corresponds to the typical variety. However, γ *gracile* is described from two collections, the first being the same as *G. strigosum*: “In dumetis Pe-ngay-tze, supra Houang-kia-pin; fl. fr. 4 sept. 1882 (Delavay, *Geranium*, n. 2; in monte Che-tcho-tze (id).” This strongly suggests that Franchet considered such variety as the typical, as Knuth (1912) indicated. Therefore, I have lectotypified *G. strigosum* on *Delavay Geranium* n. 2. The result is that *G. strigosum* var. *gracile*, typified by Yeo (1992) on the same specimen, becomes homotypic of *G. strigosum*. Yeo (1992) was aware of this coincidence of localities but considered the type of *G. strigosum* as non vidi.

Wu (1984) proposed the combination *Geranium strictipes* var. *grandiflorum*, which is not validly published according to Articles 41.5 and 41.6 of the ICN (McNeill et al., 2012), because he cited the basionym and its author but without reference to its place of valid publication.

Additional specimens examined. CHINA. **Sichuan:** Jiulong Xian, betw. city Jiulong & Yalong Jiang, right side hwy. going toward Yalong Jiang, 28°40'N, 101°34'E, Boufford et al. 33029 (A, MA); Muli Xian, border of Muli Xian & Yanyuan Xian on E side rd. (hwy. 216), 27°41'N, 101°13'E, D. E. Boufford et al. 42801 (MA); ad oppidum Yenyüen regione, in steppis ad vic Schuitangdse, 27°27'N, 101°38'E, H. F. Handel-Mazzetti 2830 (WU); ad oppidum Yenyüen regione, inter vicos Dnörlliandgse et Hungga, 27°27'N, 101°38'E, H. F. Handel-Mazzetti 2888 (WU); inter oppidum Yenyüen et flumen Yalung, 27°38'N, 101°18'E, H. F. Handel-Mazzetti 5410 (W, WU); Muli, 27°50'N, 101°15'E, F. Kingdon Ward 4040 (E), 4279 (E); Kientchang, Mienming, 28°33'N, 102°10'E, A. F. Legendre 1425 (P); Szechuan asutral inter Yenyuan hsien et Yung ming, pr. pagum Hunka, 27°38'N, 101°18'E, C. Schneider 1171 (G, GH). **Yunnan:** Diqing pref., betw. Zhongdian & Jiulong, 27°42'N, 100°1'E, B. Aldén et al. 1268 (E); Zhongdian, rd. to Haba Shan, 27°33'N, 100°1'E, *Alpine Garden Soc. Exp.* 247 (E); col de Koua-la-po, 26°6'N, 99°57'E, P. J. Delavay 2165 (K, P); col de Yen-tze-hay, 26°21'N, 100°6'E, P. J. Delavay s.n. (K, P); W flank of Haba Snow range, 27°20'N, 100°4'E, K. M. Feng 1367 (A); Lichiang range, 27°25'N, 100°5'E, G. Forrest 10340 (BM); Lichiang range, 27°25'N, 100°8'E, G. Forrest 10370 (BM,

E, GH); hills forming the E boundary of the Lichiang valley, 27°25'N, 100°8'E, G. Forrest 6113 (BM, E, P); pr. urbem Lidjiang (Likiang) in monte Yülung-schan, 27°10'N, 100°20'E, H. F. Handel-Mazzetti 3798 (W, WU); Jade Dragon mtn., 27°5'N, 100°10'E, S. Y. Hu & Y. C. Kong Y080 (A); Lijiang Co., Yuhu, Xuesong Cun, Beisha Xiang, foot of Mt. Yulongxue, 27°7'N, 100°10'E, F. Konta & H. Koyama 2469 (A); Kunmin, near Hua-ji-gou, 25°2'N, 102°43'E, J. Murata & F. Yamazaki 9251 (MO); on Ma Huang Paddock, bank of Nguluke, Lichiang Snow range, 27°0'N, 100°10'E, J. F. Rock 4352 (E, US); Yangtze watershed, Likiang, E slopes of Likiang Snow Range, 27°20'N, 100°8'E, J. F. Rock 4443 (E, GH, NY, P, US); Lichiang ad pagum Ugu leh keh, 27°0'N, 100°10'E, C. Schneider 1864 (G, GH); prope Linkiang, 27°0'N, 100°10'E, C. Schneider 1869 (G, GH, K); Lijiang Co., Yulong Shan, above Gao Shan Zhi Yu Yan, 27°10'N, 100°20'E, *Sino-Brit. Lijian Exped.* 1256 (K); Lijiang Co., Yulong Shan, above Gao Shan Zhi Yu Yan, 27°10'N, 100°20'E, *Sino-Brit. Lijian Exped.* 1266 (E); Yunnan Findspot, Lijiang, Yulong Shan, Ganghoba [cultivado en Wakehurst], 27°10'N, 100°20'E, *Sino-Brit. Lijian Exped.* 603 (MA); Li-kiang Hsien, 27°0'N, 100°10'E, C. W. Wang 70555 (A); Li-kiang Hsien, 27°0'N, 100°10'E, C. W. Wang 70934 (A); Keng-Ma, 23°31'N, 99°22'E, C. W. Wang 72927b (GH); Li-kiang Hsien, 27°0'N, 100°10'E, C. W. Wang 79873 (KUN); ciudad Lijaing, 26°53'N, 100°14'E, Q. Wang 71658 (IBSC); distr. Dali, población Jian Chuan, en el camino del pueblo Dian Nan al pueblo Ma Deng, 26°26'N, 99°55'E, *Xiangko Exp.* 243 (KUN); ciudad Lijiang, pueblo Xuesong, 27°10'N, 100°20'E, T. T. Yü 15323 (PE); ciudad Lijiang, montaña Yulong, 27°10'N, 100°20'E, A. Zhang 100312 (KUN); cerca del Jardin Botanico de Lijiang, *Zhong Dian Exp.* 606 (PE).

6. *Geranium umbelliforme* Franch., Bull. Soc. Bot. France 33: 443. 1887. TYPE: China. Yunnan: in silvis ad juga Koua-la-po, supra Hokin, 26°31'N, 100°11'E, 4 Aug. 1885, P. J. Delavay 1944 (lectotype, designated by Yeo [1992: 194], P!). Figure 13.

Perennial herbs, 28–45 cm. Stem erect, leafy, with patent, eglandular hairs 0.3–3.9 mm and patent, glandular hairs 0.7–1.8 mm. Basal leaves in a \pm persistent rosette, cauline leaves alternate in middle of shoot and opposite at apex; leaf laminae (3.7)4.1–6.9(8.4) \times 4.9–9.9 cm, palmatifid (ratio of main sinus length:middle segment length = [0.66]0.67–0.73), polygonal in outline, base cordate, pilose, with \pm appressed, eglandular hairs and plane, glandular hairs on both surfaces; segments 5, middle segment obtriangular, 8–14 mm wide at base, 7- to 15-lobed in distal half; petioles up to 20 cm, with patent, eglandular hairs 0.4–3.9 mm and patent, glandular hairs 0.6–1.8 mm; stipules 4.5–8.7 \times 1.2–2.6 mm, ovate, obtuse, free, brown, with scattered eglandular and glandular hairs on abaxial surface and margin, glabrous adaxially. Inflorescence a monochasial cyme; cymules (2)3- to 4-flowered, in loose umbel-like aggregates at top of each branch; peduncles 25–

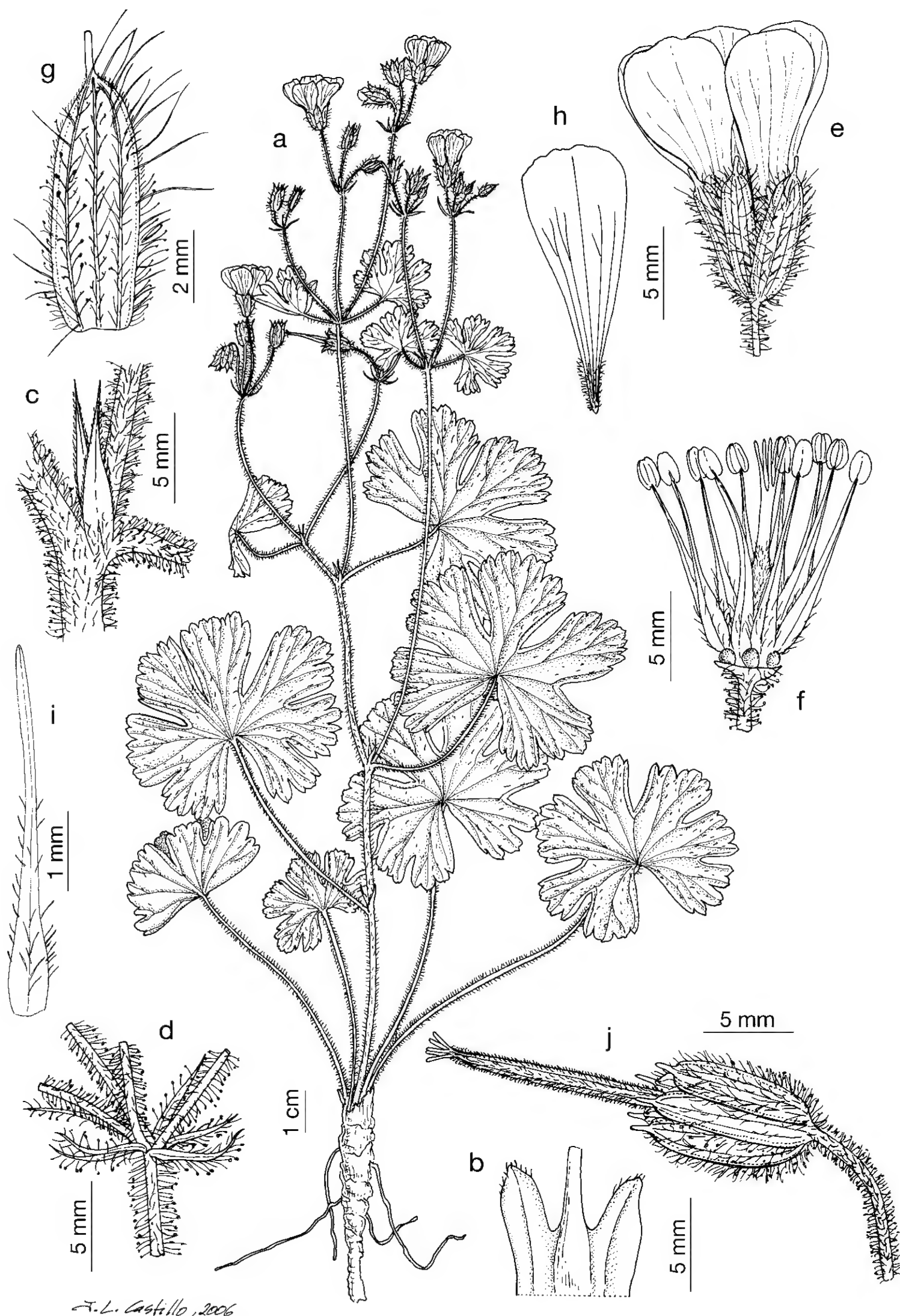


Figure 13. *Geranium umbelliforme* Franch. —A. Habit. —B, C. Stipules. —D. Bracteoles. —E. Flower. —F. Flower without petals and sepals. —G. Sepal. —H. Petal. —I. Staminal filament. —J. Fruit. E based on *G. Forrest 6195* (E).

67 mm, with patent, eglandular hairs 0.5–3 mm and patent, glandular hairs 0.6–1.8 mm; bracteoles 3.4–6 × 0.3–0.7 mm, linear-lanceolate, whorled; pedicels (5)12–34(35) mm, with patent, eglandular hairs 0.4–3.5 mm and patent, glandular hairs 0.6–1.8 mm. Flowers actinomorphic. Sepals 6.1–6.7(7.6) × 1.7–2.7 mm, lanceolate, smooth, not accrescent, with mucro 0.5–1.4 mm (ratio of mucro length:sepal length = 0.09–0.18), with patent, eglandular hairs 0.3–3.3 mm and patent, glandular hairs 0.6–1.9 mm on abaxial surface, glabrous adaxially. Petals (13.1)13.8–15.2(16.8) × 5–9 mm, erect-patent, entire or retuse, without claw, purple, hairy on base of both surfaces (mainly on adaxial one) and basal margin with hairs 0.4–1 mm. Staminal filaments 3.9–6.7 mm, lanceolate, white, pilose on abaxial surface, ciliate on proximal half, with hairs 0.3–0.9 mm; anthers 0.9–1.6 mm, unknown color. Nectaries 5, hemispheric, glabrous. Gynoecium 4.3–6.2 mm, red. Fruit 18.2–21.5 mm; mericarps 2.8–3.4 × 0.8–1.4 mm, reticulate, brown, with ± appressed, eglandular hairs 0.1–0.2 mm; rostrum 12.3–15.9 mm, with a narrowed apex 2–2.1 mm, with patent, eglandular hairs 0.3–0.4 mm, and sometimes scattered, patent, glandular hairs 0.2–0.3 mm; stigmatic remnants 1.1–1.5 mm, with 5 glabrous lobes. Seeds unknown. Chromosome number not known.

Additional illustrations. Franchet (1889, tab. 25); Wu and Chen (1991: 94, tab. 28, figs. 1–5).

Phenology. *Geranium umbelliforme* has been collected in flower from July to August.

Distribution and habitat. *Geranium umbelliforme* is present in Sichuan and Yunnan Provinces in southwestern China, in meadows and forest edges among limestone cliffs. The species is found at altitudes of 3000–3380 m. Figure 7.

Discussion. In its general aspect *Geranium umbelliforme* is similar to *G. polyanthes*. They share a similar inflorescence structure and alternate cauline leaves. Nonetheless, *G. umbelliforme* has cymules with usually well-developed peduncles and longer pedicels, resulting in a lax inflorescence. Petals of *G. umbelliforme* are longer and narrower than those of *G. polyanthes* and the narrowed apex of the fruit rostrum is longer. Additionally, the leaves of *G. umbelliforme* are longer and with more lobes per segment, bracteoles are narrower, sepal mucro is longer, and staminal filaments and anthers are longer. These features overlap to some degree.

Among the few available collections, the underground parts are poorly represented. Nevertheless,

Geranium umbelliforme appears to have a more or less vertical rootstock. Only two specimens had fruits and the seeds are unknown because these fruits were immature. Thus, more collections may help to clarify the degree of character variation in both rootstock and fruits within this species.

The ranges of these species do not overlap but are close; *Geranium polyanthes* occurs in the Himalaya in a zone about 2000 km from Uttaranchal in North India to Yunnan Province in China, whereas *G. umbelliforme* appears easternmost, in Yunnan and Sichuan Provinces.

Additional specimens examined. CHINA. **Sichuan:** Muli, 27°50'N, 101°15'E, *J. Kingdon Ward 4543* (E); Muli, mtns. of Kulu, 27°50'N, 101°15'E, *J. F. Rock 18042* (E, GH). **Yunnan:** au col de Koua-la-po, point culminant de la rte. de Ta-li à Hokin, 26°26'N, 100°6'E, 24 July 1883, *P. J. Delavay s.n.* (P); Yunnan, E flank of the Lichiang Range, 27°30'N, 100°8'E, *G. Forrest 6195* (BM, E, K, P); prefectura Dali, Henqing, pueblo Songgui, mtn. Maer Shan Yanzidong, 26°22'N, 100°13'E, *Jinshajiang Exp. 4759* (KUN); prefectura Dali, Henqing, pueblo Machang Baishanmu, 26°17'N, 100°16'E, *R. C. Ching 23481* (PE).

7. *Geranium wardii* Yeo, Notes Roy. Bot. Gard. Edinburgh 34(2): 195. 1975. TYPE: Burma. West Central Burma: Mt. Victoria, 21°14'N, 93°55'E, 26 Oct. 1956, *F. Kingdon-Ward 22760* (holotype, BM!; isotypes, CGG not seen, GB image!). Figure 14.

Perennial herbs, 23–30 cm. Stem erect or ascending, leafy, with patent, scattered, eglandular hairs 0.2–0.9 mm. Basal leaves in a deciduous rosette, cauline leaves opposite; leaf laminas 2.2–3.3 × 2.7–4.7 cm, palmatifid (ratio of main sinus length:middle segment length = 0.57–0.60), polygonal in outline, base cordate, pilose, with ± appressed, eglandular hairs and plane, glandular hairs on both surfaces; segments 5, middle segment obtriangular, 5.4–7.7 mm wide at base, 7- to 8-lobed in distal half; petioles up to 6 cm, with patent, eglandular hairs 0.3–0.4 mm and patent, glandular hairs 0.7–1 mm; stipules 2.8–5.5 × 1.7–2.4 mm, ovate, obtuse, free, brown, with eglandular and glandular hairs on margin. Inflorescence a dichasial cyme with monochasial branches; cymules 2-flowered, solitary; peduncles 29–64 mm, with uncinat, retrorse, eglandular hairs 0.2–0.3 mm and patent, glandular hairs 0.4–0.8 mm; bracteoles 4–4.5 × 0.9–1.2 mm, broadly lanceolate, obtuse, whorled; pedicels 18–38 mm, with uncinat, retrorse, eglandular hairs 0.2–0.3 mm and patent, glandular hairs 0.7–0.8 mm. Flowers actinomorphic. Sepals 6.6–11 × 3.4–4 mm, lanceolate, smooth, not accrescent, with mucro 1.1–1.2 mm (ratio of mucro length:sepal length =

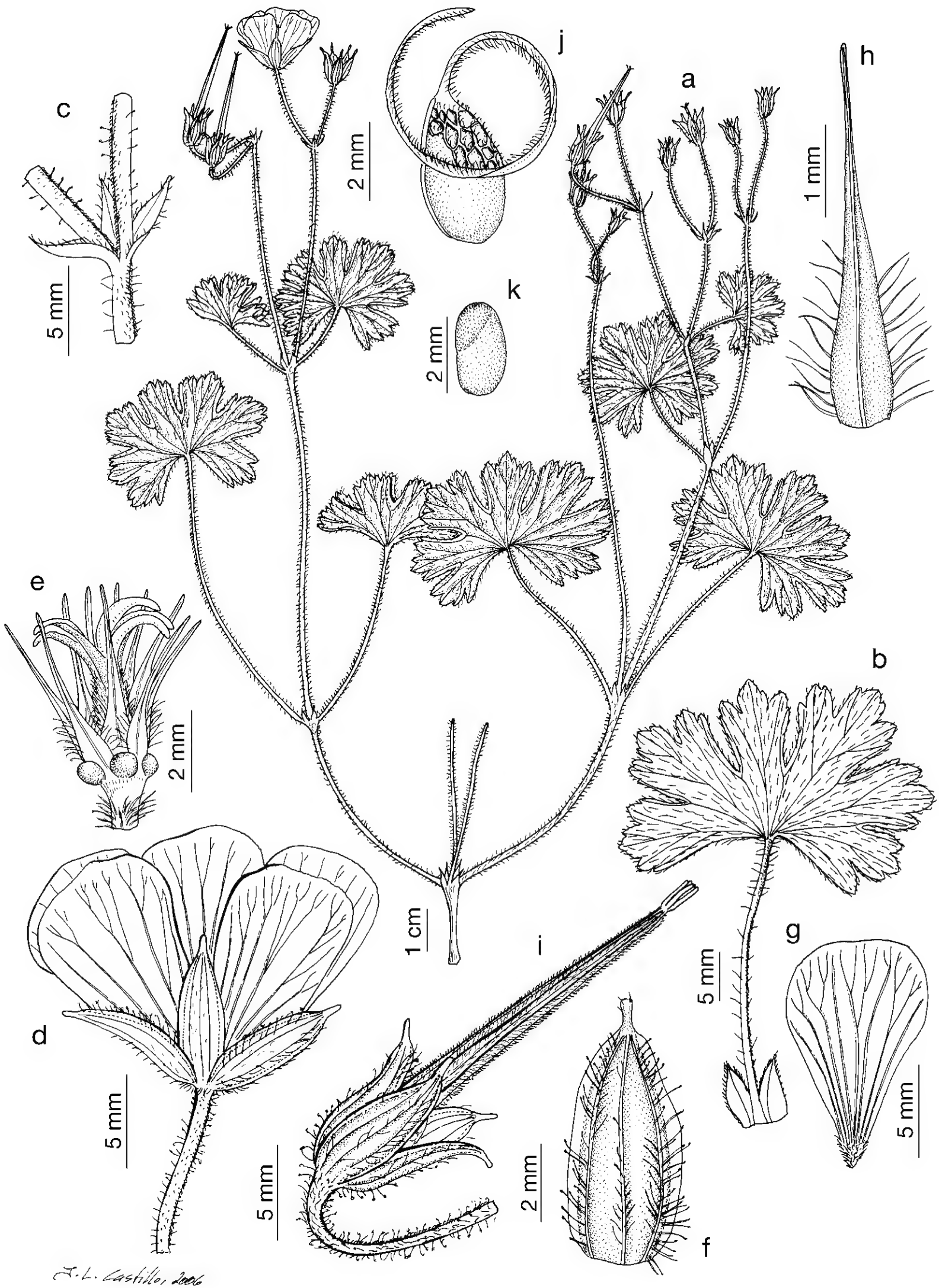


Figure 14. *Geranium wardii* Yeo. —A. Habit. —B. Leaf. —C. Bracteoles. —D. Flower. —E. Flower without petals and sepals. —F. Sepal. —G. Petal. —H. Staminal filament. —I. Fruit. —J. Mericarp. —K. Seed. Based on *F. Kingdon-Ward* 22760 (BM).

0.10–0.18), with \pm patent, eglandular hairs 0.2–0.3 mm and patent, glandular hairs 1–1.3 mm on abaxial surface, glabrous adaxially. Petals 12.6–13.4 \times 7.8–8.3 mm, erect-patent, entire, without claw, purple, hairy on base of adaxial surface, glabrous on abaxial surface, ciliate on basal margin, with hairs 0.3–0.5 mm. Staminal filaments 3.3–4 mm, lanceolate, purple, pilose on abaxial surface, ciliate on proximal half, with hairs 0.3–0.5 mm; anthers 1.4–1.5 mm, purple. Nectaries 5, hemispheric, glabrous. Gynoecium 4.4–5 mm, unknown color. Fruit 23–26 mm; mericarps 3.4–5.2 \times 1.2–1.9 mm, reticulate, brown, with \pm appressed, eglandular hairs 0.2–0.3 mm; rostrum 16–16.5 mm, without narrowed apex, with patent, eglandular hairs 0.2–0.3 mm; stigmatic remnants 1.9–2.5 mm, with 5 glabrous lobes. Seeds 2.7–2.8 \times 1.5–1.6 mm, smooth, brown. Chromosome number not known.

Phenology. *Geranium wardii* was collected in flower in October.

Distribution and habitat. *Geranium wardii* is present in central-western Burma, on turf slopes at altitudes of 2500–2800 m. Figure 5.

Discussion. *Geranium wardii* is only known from the type, a flowering and fruiting collection. However, the specimens lack the rootstock and roots. *Geranium wardii* shares with *G. strictipes* and *G. hispidissimum* opposite leaves and inflorescence in dichasial cyme, with monochasial branches. The leaves of *G. hispidissimum* are similar to those of *G. wardii* in the degree of division but have more lobes per segment and a denser indumentum. The petals of *G. wardii* and *G. strictipes* are longer than those of *G. hispidissimum*. In contrast, the sepal mucro of *G. wardii* is shorter than that of *G. strictipes* or *G. hispidissimum*, and the nectaries are glabrous (with a tuft of hairs in *G. strictipes* and *G. hispidissimum*). The stipules of *G. wardii* are ovate with an obtuse apex and resemble those of *G. nakaoanum*, *G. polyanthes*, and *G. umbelliforme*; in *G. strictipes* and *G. hispidissimum* the stipules are lanceolate.

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- Xiangko Exp. 243 (5).
- Yon, B. 192 (4); 426 (1); Yü, T. T. 1541 (6); 6670 (5); 7491 (5); 15323 (5); 19713 (1); 22528 (1).
- Zhang, A. 100312 (5); Zhong Dian Exp. 606 (5).

Appendix 1. Index of collectors.

Collections are listed alphabetically by first collector's last name. Numbers in parentheses refer to the corresponding species in the text.

Aldén, B. et al. 1268 (5); Alpine Garden Soc. Exp. 247 (5); Anderson, M. 6 (1); Anderson, T. 412 (1).

FLOWERING PHENOLOGY AND FLORAL VISITORS IN DISTYLOUS POPULATIONS OF *PSYCHOTRIA* *CARTHAGENENSIS* (RUBIACEAE) IN BRAZILIAN CERRADO¹

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Araújo³

ABSTRACT

Flowering synchrony has a relevant role in pollinator attraction. In distylous species, synchronous blooming between individuals of both morphs means that the chances of intermorph crosses are increased, which is important for the maintenance of the heterostylous system. The aim of the present study was to describe the flowering phenology and the behavior of the floral visitors in three populations of *Psychotria carthagenensis* Jacq. (Rubiaceae) between January 2008 and January 2010. Flower and pollinator censuses were conducted at three urban forest fragments in Brazil. *Psychotria carthagenensis* flowering occurred between October and December, with a high degree of synchrony within populations as well as between floral morphs. The exotic *Apis mellifera* L. (Apidae) was the main pollinator in the three populations. A high degree of similarity was found in the behavior of floral visitors as well as in nectar production. Visitation rates did not differ between floral morphs. Similar floral recompenses (flower availability and nectar) as well as no preference in pollinators' visiting are thought to be contributing to a greater intermorph visitation to pin and thrum flowers in *P. carthagenensis*.

Key words: Distyly, floral polymorphism, flowering synchrony, heterostyly, pollination.

Heterostyly is a genetic polymorphism characterized by the occurrence of two (distyly) or three (tristyly) floral morphs in a given population (Barrett, 1992a). Heterostylous populations could present an equal balance in morph ratio (isoplethy) as well as deviation of morph frequencies in a 1:1 ratio (anisoplethy). Within the Rubiaceae, distyly is mainly documented in the Rubioideae and is characteristic of the Psychotrieae (Barrett & Richards, 1990). In typically distylous species among the angiosperms, pin flowers have long styles and short stamens, whereas thrum flowers have short styles and long stamens (Ganders, 1979).

Beyond the reciprocal positioning of the anthers and stigmas and heteromorphic incompatibility, ancillary polymorphisms occur in typical distylous systems, such as morph-specific differences in corolla length, morphology and quantity of pollen grains, and size and morphology of the stigma and

stigmatic papillae (Vuilleumier, 1967; Ganders, 1979; Barrett & Richards, 1990; Hamilton, 1990; Castro et al., 2004). These differences between floral morphs can lead to differences in the most effective pollen vectors (Lau & Bosque, 2003), which, in turn, can result in loss or modification of heteromorphic incompatibility (see Pérez-Alquicira et al., 2010; Sosenski et al., 2010). Variations in floral morphology, incompatibility systems, and morph ratios between populations are well-documented for distylous species (e.g., Sobrevilla et al., 1983; Li & Johnston, 2001; Sakai & Wright, 2008; Ferrero et al., 2011a, 2011b).

Heterostyly traditionally has been seen as a mechanism that promotes cross-pollination and reduces pollen waste (Darwin, 1877; Lloyd & Webb, 1992a, 1992b), thereby suggesting disassortative pollination, in which there is greater pollen flow to the opposing morph (Darwin, 1877; Charlesworth &

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Charlesworth, 1979; Lloyd & Webb, 1992b; Barrett, 2002). If pollen flow is disassortative and both morphs have equal functional potential, both are expected to exhibit equivalent male and female reproductive success (García-Robledo, 2008). In distylous species, asymmetrical pollen flow between morphs is common (Lau & Bosque, 2003). Deviations in the pollen flow pattern in heterostylous species have generally been associated with the absence of specialized pollinators (Ornduff, 1971; Björkman, 1995) as well as alterations in the foraging behavior of pollinators (Wolfe & Barrett, 1989). Also, variations in floral display may account for differences between morphs regarding pollen deposition rate and female reproductive success (Brys & Jacquemyn, 2010), due to the effects of floral display on the attraction and visitation rates of pollinators. Therefore, understanding how plant-pollinator interactions influence reproductive success is essential for understanding the factors that affect the maintenance and evolution of heterostyly (Thompson & Dommée, 1993; Stone, 1996).

The periodicity of flowering is critical to reproduction for the plants (Rathcke & Lacey, 1985) and is regulated by endogenous characteristics related to biotic and abiotic factors that are selective to flowering development (Van Schaik et al., 1993). Additionally, there is a consensus that floral display affects the fitness of the plants through pollination processes (Van Schaik et al., 1993; Fenner, 1998; Sakai, 2001). At the population level, for instance, some degree of flowering synchrony is needed so that floral display and pollinator attraction are enhanced, thereby increasing the chance of crossing between individuals (Rathcke & Lacey, 1985). In distylous species, flowering synchrony between individuals of both morphs means that the chances of intermorph crosses are increased, which is integral to the maintenance of the heterostylous system (Ganders, 1979). The effectiveness of pollination depends also on the attractiveness of floral resources offered, nectar being the resource most often presented by distylous species (Ganders, 1979). Differences in nectar composition and volume in distylous species are unusual (Ree, 1997; Legee & Wolfe, 2002; Lau & Bosque, 2003), but when they occur it is possibly due to phenotypic selection. In this instance, the pollinators respond by visiting more frequently flowers of the morph that produces the more abundant nectar (Ornelas et al., 2004; Cawoy et al., 2006). Resulting differences in visiting frequencies between floral morphs could have consequences for the maintenance of isoplethic ratios in these populations (Wolfe & Barrett, 1987).

The distylous species *Psychotria carthagenensis* Jacq. is a shrub measuring 2–3 m in height that occurs from the United States to Argentina (Hamilton, 1990). In Brazil, previous studies addressing the floral morphology and reproductive system in this species have recorded considerable variation in the reproductive characteristics, such as a case of homostyly in the northeastern region of the country (Demetrio & Machado, 2005), self-incompatibility in an anisoplethic population (Pereira, 2007) and in isoplethic populations (Koch et al., 2010; Faria et al., 2012) in the central-western region, and an instance of self-compatibility in a monomorphic population in the southeastern region (Consolaro et al., 2011). As a distylous species, morphs in populations of *P. carthagenensis* are expected to exhibit flowering synchrony to allow intermorph crosses. This can be facilitated further by similar flower availability, allowing floral visitors an equal opportunity to encounter both morphs. Despite the importance of these aspects, they remain unexplored in studies of distyly (see Ganders, 1979; Barrett & Richards, 1990; Barrett, 1992b, 2002), with no reports on pollinator performance in subsequent years and different populations. Thus, the present study seeks to answer the following questions in three populations that are both isoplethic and self-compatible (Faria et al., 2012): (1) what is the flowering period and the degree of flowering synchrony among *P. carthagenensis* individuals in each population?; (2) what is the degree of flowering synchrony between the two floral morphs of *P. carthagenensis* in terms of periodicity and floral display size?; (3) are there differences in nectar production between the two floral morphs of *P. carthagenensis*?; and (4) what is the degree of similarity in the pollinators' array and visitation rates between the floral morphs of *P. carthagenensis*?

MATERIALS AND METHODS

STUDY AREA

The three populations studied for *Psychotria carthagenensis* occur in savanna fragments in protected areas located within an urban matrix in the municipality of Campo Grande (approximately 700 m.s.m.), in the state of Mato Grosso do Sul, Brazil. These areas were located in the Prosa State Park (PSP, 135 ha, 20°27'00"S, 54°33'46"W), in the Reserve of the Universidade Federal de Mato Grosso do Sul (UFMS, 35 ha, 20°29'58"S, 54°36'50"W), and in the Reserve of the Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA, 175 ha, 20°25'41"S, 54°43'03"W), which are separated from each other by a mean distance of 12.45 km. Plants of

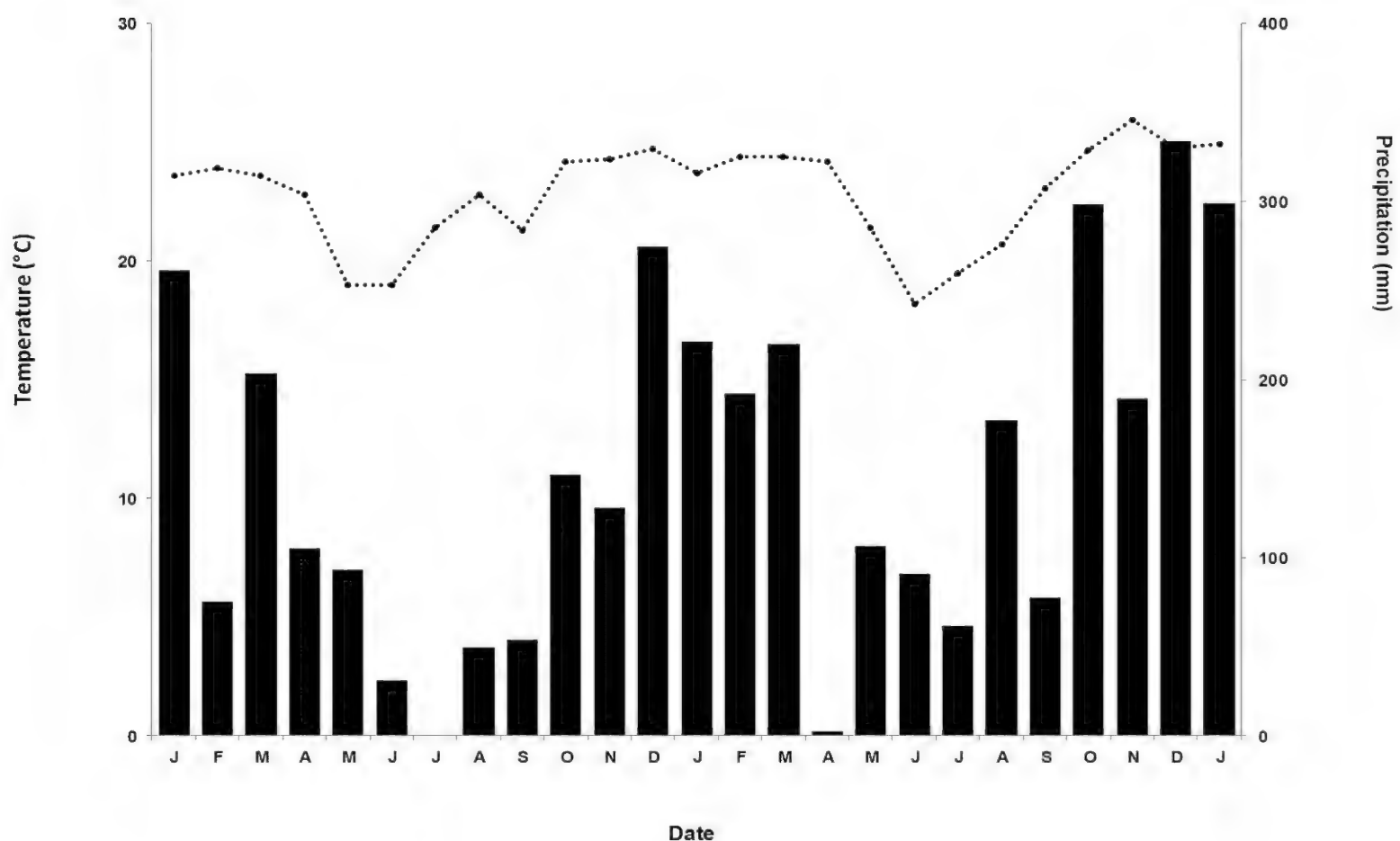


Figure 1. Climatic data from January 2008 to January 2010 for the municipality of Campo Grande, Mato Grosso do Sul, Brazil. The mean monthly temperature is represented by a dotted line; accumulated monthly precipitation is represented by bars (Source: Meteorological Station of Universidade para o Desenvolvimento do Estado e da Região do Pantanal).

P. carthagenensis occur exclusively in forest understorey and preferentially in moister soils, near streams (see Faria et al., 2012 for details on plant distribution in the study sites). In the three sites, edaphic conditions are quite similar, with the soil classified as dark-red latosol (oxisol) (Theodoroviz & Theodoroviz, 2010). The climate is characterized by a pronounced dry season from May to September and a rainy season from October to April. Annual accumulated rainfall is approximately 1532 mm, and the mean annual temperature is 20° to 22°C (EMBRAPA-CNPQC, 1985). Data on monthly accumulated precipitation and mean monthly temperature for the entire study period were obtained from the Meteorological Station of the Universidade para o Desenvolvimento do Estado e da Região do Pantanal (UNIDERP) (Fig. 1).

FLOWERING PHENOLOGY AND NECTAR

Twenty *Psychotria carthagenensis* plants per floral morph in each population were randomly selected and marked for the analysis of flowering phenology. In these individuals the number of open flowers was recorded between January 2008 and January 2010. Monitoring was carried out on a monthly basis until flowering had been initiated and was then done on a fortnightly basis. The flowering pattern (duration and

frequency of the phenophase) of the populations was classified according to Newstrom et al. (1994).

In November 2009, the peak of flowering season in the three studied populations, five flowers on each of 10 randomly selected plants of each morph in each population were selected randomly for measuring nectar volume and concentration. The flowers used to measure the nectar were bagged in the bud phase, with nectar measurement performed on the following day, between 1000 hr. and 1200 hr. Anthesis in *Psychotria carthagenensis* begins approximately between 0500 hr. and 0600 hr. and similarly in both morphs (Faria et al., 2012). Most focal observations were also performed in the morning such that the values reflect the availability of nectar to floral visitors, which allowed us to compare these values with the frequency of visits in this period. Volume was determined using a micro-syringe, and the sugar concentration was determined using a pocket refractometer (Dafni et al., 2005).

FLORAL VISITORS

Census of insect visitors was carried out in the morning (0700–1200 hr.; five censuses per population in 2008 and seven in 2009) and in the afternoon (1200 hr. and 1800 hr.; one census per population in 2008 and 2009). Most observations were made in the forenoon, because previous observations had indicated

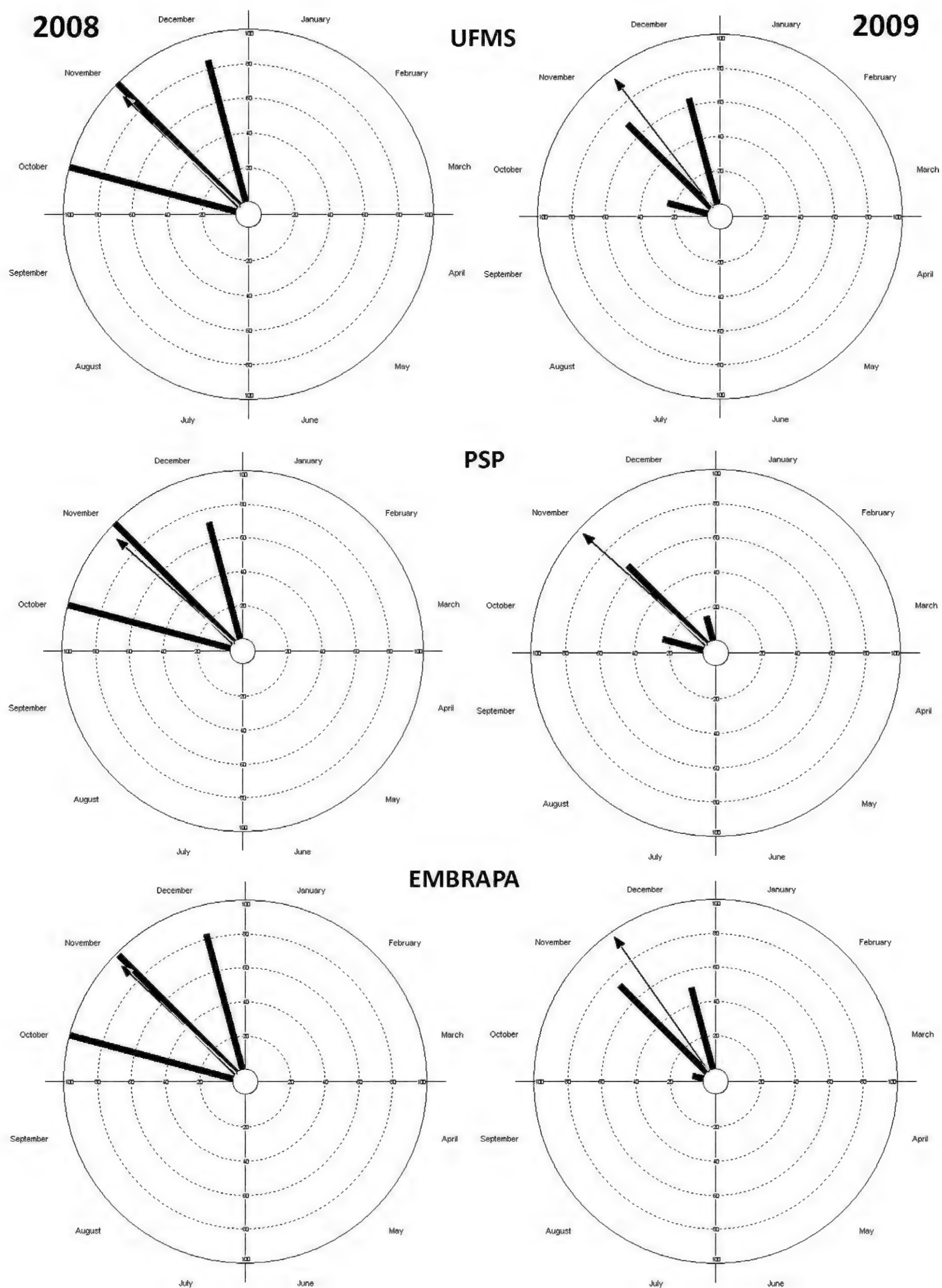


Figure 2. Circular histogram for flowering periods in three populations (UFMS, PSP, EMBRAPA) of *Psychotria carthagenensis* Jacq. in 2008 and 2009, Campo Grande, Mato Grosso do Sul, Brazil. Axes indicate frequency scale; bars indicate frequency of flowering individuals; arrow indicates mean flowering date; length indicates degree of synchrony between individuals within the population. The three studied populations are the Prosa State Park (PSP), the Reserve of the Universidade Federal de Mato Grosso do Sul (UFMS), and the Reserve of the Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA).

Table 1. Mean flowering date, synchrony (r indicates a concentration value in the mean angle; values range between 0 = absence of synchrony and 1 = complete synchrony), Rayleigh test and *P* values, with the level of data significance (< 0.05) for three populations of *Psychotria carthagenensis* Jacq. in 2008 and 2009, Campo Grande, Mato Grosso do Sul, Brazil. The Rayleigh test (z) calculates the probability (p) of the null hypothesis, which suggests that the data are evenly distributed, where z is the critical value to estimate this probability. The three studied populations are: Prosa State Park (PSP), the Reserve of the Universidade Federal de Mato Grosso do Sul (UFMS), and the Reserve of the Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA).

Year	Population	Mean date	Synchrony (r)	Rayleigh test (z)	<i>P</i> value
2008	UFMS	Nov. 3, 2008	0.924	243.242	< 0.001
	PSP	Nov. 3, 2008	0.924	232.113	< 0.001
	EMBRAPA	Nov. 1, 2008	0.931	243.614	< 0.001
2009	UFMS	Nov. 16, 2009	0.915	133.983	< 0.001
	PSP	Nov. 5, 2009	0.930	90.751	< 0.001
	EMBRAPA	Nov. 19, 2009	0.954	118.352	< 0.001

greater pollinator activity during this time (Rogério R. Faria, pers. obs.). The visitation rate (number of visitors/number of flowers observed/hour) was calculated through sessions of focal observations performed in the three populations. Each session was made up of focal observations of five randomly chosen plants of each morph. These observations lasted 15 minutes for each individual plant and were carried out every two weeks. Each observation session lasted 75 minutes per morph per population. Six censuses were performed in 2008 and eight were performed in 2009, totaling 360 hours of focal observations. According to a visitor's behavior, insect visits were classified as: (1) pollinating (contact with anthers and stigma) or (2) nectar thieving or robbing (no contact with anthers and stigma). Specimens of floral visitors were captured during the visits with the aid of a net and/or plastic bags for subsequent identification to the highest possible level of taxonomic resolution. Insect and plant vouchers are deposited at the Universidade Federal de Mato Grosso do Sul (Coleção Zoológica de Referência da Universidade Federal de Mato Grosso do Sul [ZUFMS] and Herbário da Fundação Universidade Federal de Mato Grosso do Sul [CGMS], respectively) (Appendix 1).

STATISTICAL ANALYSES

In order to determine the flowering pattern of the two floral morphs of *Psychotria carthagenensis*, circular histograms were constructed with the frequency distribution of flowering individuals in 2008 and 2009. For this analysis, days are converted to angles, from 0° (January) to 330° (December), in intervals of 30°. The Rayleigh test (z) calculates the probability (*P*) of the null hypothesis, which states that data are evenly distributed. The same test indicates the occurrence of periodicity in irregularly sampled data, in order to calculate the mean flowering date for each population and the concentration (r value, in this study

considered as intra-population flowering synchrony) of blooming individuals around this mean date (Morellato et al., 1989), using the Oriana 2.0 program (Kovach, 2004). Thus, a *P* value below the level of significance (< 0.05) indicates that the data were not distributed evenly and offers evidence of a preferred direction. The length of the vector on the graph is related to the concentration value (r value, ranging from 0 to 1), and the arrow points to the mean angle (mean date) of the frequency distribution (Kovach, 2004). Floral display size was considered in each population as the maximum of flower production in each individual. Then, floral display size was compared between morphs in each population using a student *t* test. This test was also used to determine whether differences exist in the volume (μL) and concentration (%) of sugars in the nectar of pin and thrum flowers for each population separately.

Visitation rates for both morphs were calculated and compared separately by year and population using the non-parametric Mann-Whitney *U* test with the Bioestat 4.0 program (Ayres et al., 2005). The Morisita quantitative similarity index was used to calculate the similarity in the composition of floral visitors' species between morphs for each population and each year, with the aid of the Biodap program (Harmer et al., 2001). For this analysis, we calculated the visit frequency (number of visits of a species/total number of visits of all species per morph) of each floral visitor.

RESULTS

FLOWERING PHENOLOGY AND NECTAR

The flowering of *Psychotria carthagenensis* occurred between October and December in the three studied populations in both years (Fig. 2). Intra-population synchrony values (r) ranged from 0.915 to 0.954, and the mean date was between November 1 and 19. Significant values in the analyses were found in all cases (Table 1).

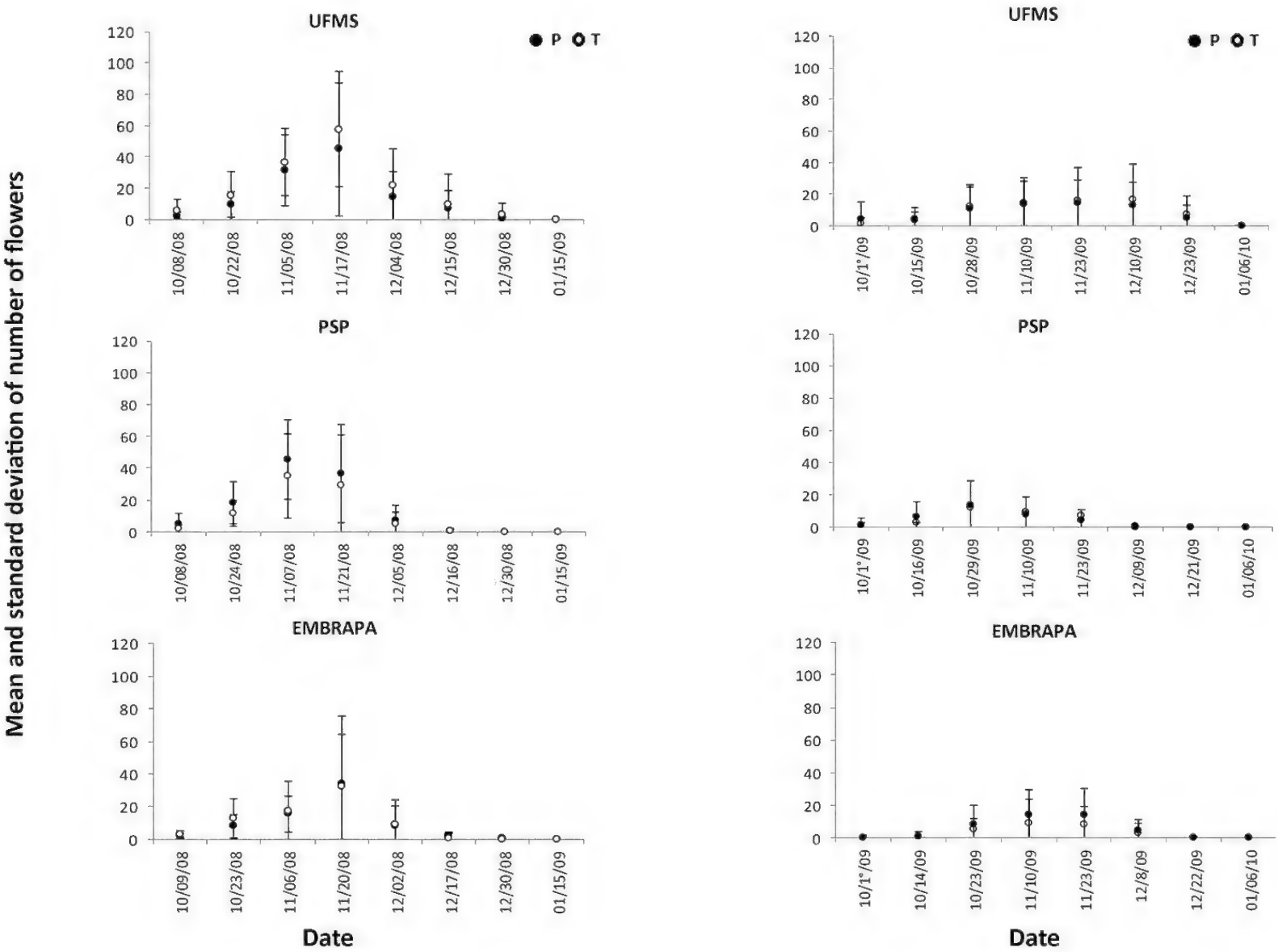


Figure 3. Mean and standard deviation of number of flowers of pin (P) and thrum (T) morphs in the three populations (UFMS, PSP, EMBRAPA) of *Psychotria carthagenensis* during flowering periods in 2008 and 2009, Campo Grande, Mato Grosso do Sul, Brazil. The three studied populations are the Prosa State Park (PSP), the Reserve of the Universidade Federal de Mato Grosso do Sul (UFMS), and the Reserve of the Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA). Closed circles represent mean values for P; open circles are mean values for T.

In 2008, peak flower production (mean and standard deviation) in the three populations ranged from 34 ± 41.32 flowers to 45.45 ± 24.88 flowers in the pin morph and from 32.05 ± 32.44 flowers to 57.6 ± 36.97 flowers in the thrum morph. In 2009, maximal flower production values in the three populations ranged from 13.74 ± 15.30 flowers to 14.6 ± 15.59 flowers in the pin morph and 8.85 ± 14.65 flowers to 16.1 ± 20.65 flowers in the thrum morph in 2009 (Fig. 3). The floral display size did not differ between morphs, both in 2008 and 2009, in all populations (Table 2). Also, means and standard deviations were never close to the peak of flower production, which is evidence that some plants reach their maximum floral display outside of the population flowering peak (Table 2).

Sugar concentration (mean and standard deviation) in the nectar ranged from $14.4 \pm 5.96\%$ in the thrum morph in the UFMS population to $16.6 \pm 3.03\%$ in the pin morph in the EMBRAPA population. Nectar volume ranged from $1.5 \pm 0.68 \mu\text{L}$ in the UFMS

population to $2.4 \pm 0.52 \mu\text{L}$ in the PSP population. No statistically significant differences between morphs were detected for the concentration and volume data in any of the cases (Table 3).

FLORAL VISITORS

The highest visitation rates in 2008 were for the thrum morph in the UFMS population, for the thrum morph in the PSP population, and for the pin morph in the EMBRAPA population (Table 4). The highest visitation rates in 2009 were for the thrum morph in the UFMS population, for the thrum morph in the PSP population, and for the pin morph in the EMBRAPA population (Table 4). No significant differences were detected in the comparisons between morphs in each population (Table 4).

During the two flowering seasons (2008 and 2009), 22 floral visitors were recorded, with 14 visitors recorded in each population and only five common to all three populations. The Morisita-Horn index values

Table 2. Comparison of means and SD of floral display sizes (the maximum flower production in each individual) between pin (20 plants/population) and thrum (20 plants/population) floral morphs of three populations of *Psychotria carthagenensis* Jacq. from Campo Grande, Mato Grosso do Sul, Brazil. The three studied populations are the Prosa State Park (PSP), the Reserve of the Universidade Federal de Mato Grosso do Sul (UFMS), and the Reserve of the Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA). Student *t* test values are indicated by *t*; degrees of freedom are represented by *df*; *P* refers to values of significance.

	Population	Floral morph	Mean	SD	<i>t</i>	<i>df</i>	<i>P</i>
2008	EMBRAPA	pin	35.400	40.349	−0.149	35.847	0.883
		thrum	33.700	31.419			
	PSP	pin	53.250	12.384	0.919	26.961	0.366
		thrum	59.250	26.425			
	UFMS	pin	72.750	35.696	−1.276	24.046	0.214
		thrum	61.900	13.126			
2009	EMBRAPA	pin	17.550	16.168	−1.258	37.526	0.216
		thrum	11.450	14.442			
	PSP	pin	15.263	15.434	−0.277	36.903	0.783
		thrum	13.952	14.389			
	UFMS	pin	18.850	18.584	0.946	37.370	0.350
		thrum	24.800	21.135			

indicated a 99% similarity in the composition of visitors between the floral morphs in the UFMS population in 2008 and in the PSP and EMBRAPA populations in 2009. Ninety-one percent of similarity between morphs was recorded for the PSP population in 2008, 75% was recorded for the UFMS population in 2009, and the lowest value (21%) was recorded for the EMBRAPA population in 2008 (Table 5). The most frequent floral visitor in all populations was *Apis mellifera* L. (Apidae, honey bees), with a relative visiting frequency ranging from 1.8% to 67.6%, followed by *Augochloropsis* Cockerell (sp. indet., Halictidae, sweat bees), with a relative visiting frequency ranging from 1.8% to 17.6%. In particular, *Apis mellifera* showed some preference for thrum

flowers, except in 2009 for the UFMS population (Table 5).

Among all the insects recorded in the flowers of *Psychotria carthagenensis* (Rubiaceae), only two were nectar thieves—ants and beetles. One beetle species (sp. indet., Curculionidae) and unidentified ants, including one species in *Camponotus* Mayr (Formicidae), visited flowers without coming into contact with the anthers in the thrum floral morph or the stigma in the pin morph. A weevil/snout beetle in the Curculionidae (sp. indet. 1) damaged the corolla near the flower’s base, probably feeding on flower tissue, and did not contact the reproductive structures (cf. Table 5), so it acted as a nectar robber.

Table 3. Mean and SD of nectar volume (μL) and concentration (%) in pin (five flowers/10 plants/population) and thrum (five flowers/10 plants/population) morphs of three populations of *Psychotria carthagenensis* Jacq., from Campo Grande, Mato Grosso do Sul, Brazil. The three studied populations were the Prosa State Park (PSP), the Reserve of the Universidade Federal de Mato Grosso do Sul (UFMS), and the Reserve of the Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA). Student *t* test values are indicated by *t*; degrees of freedom are represented by *df*; *P* refers to values of significance.

Population	Nectar	Mean (± SD)	<i>t</i>	<i>df</i>	<i>P</i>
PSP	volume	pin, 2.1 μL (0.65)	−0.213	98	0.832
		thrum, 2.4 μL (0.52)			
	concentration	pin, 15.5 μL (3.30)	−1.551	98	0.124
		thrum, 14.6 μL (2.44)			
EMBRAPA	volume	pin 2.3 μL (0.50)	−1.124	98	0.264
		thrum, 2.2 μL (0.44)			
	concentration	pin, 16.6 μL (3.03)	−1.492	98	0.139
		thrum, 15.6 μL (3.39)			
UFMS	volume	pin, 1.5 μL (0.68)	1.059	98	0.292
		thrum, 1.6 μL (0.78)			
	concentration	pin, 14.6 μL (5.87)	−0.169	98	0.866
		thrum, 14.4 μL (5.96)			

Table 4. Range and median of visitation rates (number of visits/number of flowers/hour) between pin and thrum morphs of three populations of *Psychotria carthagenensis* Jacq. in 2008 and 2009, Campo Grande, Mato Grosso do Sul, Brazil. The three studied populations are the Prosa State Park (PSP), the Reserve of the Universidade Federal de Mato Grosso do Sul (UFMS), and the Reserve of the Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA). Mann-Whitney values are indicated by *U*; degrees of freedom are represented by *df*; *P* refers to values of significance.

Year	Population	Morph	Range	Median	<i>U</i>	<i>df</i>	<i>P</i>
2008	EMBRAPA	pin	0.10–0.38	0.25	12.000	1	0.34
		thrum	0.04–0.22	0.19			
	PSP	pin	0.07–0.25	0.20	19.000	1	0.87
		thrum	0.00–1.05	0.25			
	UFMS	pin	0.01–0.72	0.19	21.000	1	0.63
		thrum	0.03–0.78	0.16			
2009	EMBRAPA	pin	0.00–0.94	0.11	28.000	1	0.67
		thrum	0.00–0.88	0.06			
	PSP	pin	0.00–0.33	0.16	41.500	1	0.29
		thrum	0.00–0.57	0.14			
	UFMS	pin	0.00–0.17	0.00	31.000	1	0.92
		thrum	0.00–0.19	0.04			

DISCUSSION

Individuals of *Psychotria carthagenensis* were highly synchronous within the populations in relation to flowering, with an annual occurrence and mean flowering date occurring in mid-November. Populations with annual flowering and intermediate duration have only one main flowering episode in a 1-year period and a phenophase lasting one to five months (cf. Newstrom et al., 1994). Flowering phenology of species in the family Rubiaceae generally exhibits different patterns with regard to period, season, and flower abundance (e.g., Castro & Oliveira, 2002; San Martin-Gajardo & Morellato, 2003; Pereira et al., 2006), and there has been a consensus that phenology in this family does not undergo phylogenetic restrictions (Wright, 1991; San Martin-Gajardo & Morellato, 2003).

The beginning of the rainy season is the period of greatest abundance of insects in the Brazilian savanna (Pinheiro et al., 2002), and it is also normally associated with an increase in temperature and photoperiod, resulting in a phase of greatest reproductive and vegetative activity (Morellato, 1992; Morellato & Leitão-Filho, 1992). These characteristics indicate that both biotic and abiotic factors could exert selective pressure on the phenological pattern of *Psychotria carthagenensis*.

The synchrony presented by the *Psychotria carthagenensis* populations, with regard to both flowering season and intensity, favored greater intermorph floral visitation rates, as it allowed an equal probability of visitors for both floral morphs (in the case of isoplethic populations), an important factor to the stability of the heterostylous system

(Ganders, 1979; Thompson & Dommée, 1993). Although important to the attraction of visitors and intermorph pollen flow, the similarity in floral display between floral morphs alone does not ensure similarity in reproduction success between morphs (Contreras & Ornelas, 1999). Actually, one of the major causes of morph-specific difference in reproductive success has been noted as the difference in the strength of heteromorphic incompatibility systems between floral morphs (Brys et al., 2008; Hodgins & Barrett, 2008). However, this difference was not detected here for *P. carthagenensis*, and, despite being isoplethic and presenting high morphological reciprocity between floral morphs, the studied populations are self-compatible and compatible within plants of the same morph (see Faria et al. [2012] for details on reproductive biology of *P. carthagenensis*).

The similarity in the reward offered to insect visitors by both floral morphs in *Psychotria carthagenensis* may have been responsible for the correspondence in the visiting patterns found in the populations. Indeed, no preference for one morph over another is expected when there is no difference in the volume and concentration of sugars (Weller, 1981; Wolfe & Barrett, 1987) or in the offer of flowers (Ganders, 1979) between floral morphs of distylous species. Exceptionally, *Apis mellifera* makes an apparent higher number of visits to thrum flowers. This preference by *A. mellifera* for thrum flowers, when both morphs present similar quantity and quality of nectar, as recorded in the studied populations, probably is due to spatial distribution of morphs and/or floral display in the neighborhood.

Table 5. Insect visitors and their relative frequency on flowers (number of visits of a given species/total number of visits of all species per morph) in pin and thrum morphs of three populations (Reserve of the Universidade Federal de Mato Grosso do Sul [UFMS], Prosa State Park [PSP], Reserve of the Empresa Brasileira de Pesquisa Agropecuária [EMBRAPA]) of *Psychotria carthagenensis* Jacq. during flowering periods in 2008 and 2009, Campo Grande, Mato Grosso do Sul, Brazil. The similarity value (Morisita-Horn index) between morphs is presented for each population in a given year.

Visitors	2008						2009					
	UFMS		PSP		EMBRAPA		UFMS		PSP		EMBRAPA	
	Pin	Thrum	Pin	Thrum	Pin	Thrum	Pin	Thrum	Pin	Thrum	Pin	Thrum
APIDAE												
<i>Apis mellifera</i> L.	29.2	47.3	17.3	67.6	1.8	15.2	32.8	23.2	33.5	49.1	36.7	39.2
<i>Bombus</i> L., sp. indet. 1								4.0				
<i>Bombus</i> , sp. indet. 2	1.9	3.0	0.4					3.2				
<i>Bombus</i> , sp. indet. 3					14.6							
<i>Exomalopsis</i> Spinola, sp. indet.						4.3					1.4	4.9
<i>Lophopedia</i> Michener & Moure, sp. indet. 1	0.4	0.4				1.2						
<i>Lophopedia</i> , sp. indet. 2			0.4		9.1	2.4						
<i>Paratetrapedia</i> Moure, sp. indet.	0.8	0.8	0.4	0.4	3.0	1.2		1.6		0.9	1.6	1.1
<i>Paratrigona lineata</i> Spinola			0.7		6.1	3.0			0.9	1.3	3.8	0.5
<i>Tetrapedia</i> Klug, sp. indet.					0.6	1.8			0.4	1.8	1.1	2.7
<i>Xylocopa</i> Latreille, sp. indet.							9.6					
HALICITIDAE												
<i>Augochloropsis</i> Cockerell, sp. indet.	5.7	3.4		1.8	14.6		1.6	17.6	5.8	3.1	2.7	2.2
DROSOPHILIDAE												
<i>Drosophila</i> Fallén, sp. indet.			0.4									
NYMPHALIDAE												
<i>Hypoleria lavinia</i> Hewitson							3.2					
LEPIDOPTERA												
<i>Lepidoptera</i> , sp. indet. 1		2.7	0.4	3.2				0.8	0.4			
<i>Lepidoptera</i> , sp. indet. 2					5.5	1.2						0.5
VESPIDAE												
Vespidae, sp. indet. 1	1.5		0.4									
CULICIDAE												
Culicidae, sp. indet. 1	0.4				1.8	2.4		1.6		1.8		0.3
FORMICIDAE												
* <i>Camponotus</i> Mayr, sp. indet.		1.1	0.4									
* <i>Formicidae</i> , sp. indet. 1					0.6							
CURCULIONIDAE												
* <i>Curculionidae</i> , sp. indet. 1		0.4	0.7		0.6							
NI		1.1	5.6	0.4	1.2	7.3		0.8		0.9	1.1	
Total number of visits	264		285		164		129		147		360	
Similarity (Morisita-Horn Index)	0.99		0.91		0.21		0.75		0.99		0.99	

* Nectar robbers.
Abbreviation: NI, not identified.

Given the floral morphology of *Psychotria carthagenensis*, contact with stigma by most of the recorded visitors was inevitable, so the majority of these insects acted as pollinators. Highly specialized flowers are rare in the family Rubiaceae, and the most common pollinators are generalist bees (Castro & Oliveira, 2002). For the genus *Psychotria* L., butterflies, hummingbirds, and wasps have been commonly recorded visitors (Almeida & Alves, 2000; Castro & Araujo, 2004; Teixeira & Machado, 2004). A generalist pollination system could be advantageous in situations of constant disturbance (Waser et al., 1996), as occurs in forest fragments situated in

urban areas. Such fragments can serve as a refuge for anthophilous species and function as ecological islands, as favorable environments surrounded by an inadequate matrix (Cane, 2001)—civil construction in the present case. In general, the abundance of pollinators is reduced by the effect of fragmentation, especially in the reduction and isolation of the habitat (Kearns et al., 1998; Potts et al., 2010). However, the maintenance of a large number of visitors does not always signify reproductive success for plants (Gómez, 2002). In order to certify the generalization in this system, it would also be necessary to assess the effectiveness of the pollinators.

The EMBRAPA population had a low degree of similarity between floral morphs of *Psychotria carthagenensis* regarding insect visitors in 2008. This deviation may have occurred due to the quantitative nature of the similarity index used (Magurran, 1988). The two most frequent floral visitors (*Apis mellifera* and *Augochloropsis* spp.) to the thrum morph in the EMBRAPA population were not observed on the flowers of the long-style morph. Otherwise, the morphs shared eight of the 10 insect species recorded for the thrum morph and eight of the 12 species recorded for the pin morph. For distylous species, sharing the same pollinators and having similar visitation rates would allow for an increased likelihood of intermorph pollen flow (Husband & Barrett, 1992). Thus, specialization at the level of floral morph can be seen as detrimental, as leading to asymmetrical pollen flow and potential instability of the polymorphism (Wolfe & Barrett, 1987).

The similar flowering period, floral display, and visitation rates between morphs were indicative of successful intermorph pollen transfer in the studied populations of *Psychotria carthagenensis*, providing evidence for functional distyly in this species. However, further conclusions from these results are limited. Future studies designed for evaluating pollen flow rates between floral morphs are still necessary to better understand disassortative mating in *P. carthagenensis*.

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Appendix 1. Voucher numbers of collected specimens at the three studied populations: Prosa State Park (PSP), the Reserve of the Universidade Federal de Mato Grosso do Sul (UFMS), and the Reserve of the Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA). Insects were deposited at Coleção Zoológica de Referência da Universidade Federal de Mato Grosso do Sul (ZUFMS) and plants in the Herbário da Fundação Universidade Federal de Mato Grosso do Sul (CGMS).

Specimens	Collector	Voucher number	Population
<i>Psychotria carthagenensis</i> Jacq.	R. R. Faria	52629, 52630	EMBRAPA
<i>Psychotria carthagenensis</i>	R. R. Faria	52633, 52634	PSP
<i>Psychotria carthagenensis</i>	R. R. Faria	52631, 52632	UFMS
Apidae not identified	R. R. Faria	HYM00285	EMBRAPA
Apidae not identified	R. R. Faria	HYM00270, HYM00272, HYM00275, HYM00276, HYM00277, HYM00278	UFMS
<i>Augochloropsis</i> Cockerell spp.	R. R. Faria	HYM00282, HYM00283, HYM00284	EMBRAPA
<i>Augochloropsis</i> spp.	R. R. Faria	HYM00287, HYM00290, HYM00291, HYM00292, HYM00295	PSP
<i>Augochloropsis</i> spp.	R. R. Faria	HYM00269, HYM00274, HYM00280	UFMS
<i>Apis mellifera</i> L.	R. R. Faria	HYM00281	EMBRAPA
<i>Apis mellifera</i>	R. R. Faria	HYM00286, HYM00288, HYM00289, HYM00293, HYM00294	PSP
<i>Apis mellifera</i>	R. R. Faria	HYM00268, HYM00271, HYM00273, HYM00279	UFMS

A CONSPECTUS OF *MYRCIA* SECT. *AULOMYRCIA* (MYRTACEAE)¹

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ABSTRACT

An annotated conspectus of 124 species is presented for *Myrcia* DC. sect. *Aulomyrcia* (O. Berg) Griseb. This list is published for use as a basis for future revisionary work and presents the species of this evolutionary group together for the first time. Publication and type information, habitat and distribution, preliminary conservation assessments, and diagnostic notes are provided for each species. In transferring species of *Calyptanthus* Sw. and *Marlierea* Cambess. to *Myrcia*, 28 new combinations are made: *Myrcia areolata* (McVaugh) E. Lucas & C. E. Wilson [= *Marlierea areolata* McVaugh], *Myrcia biptera* (Amshoff) E. Lucas & C. E. Wilson [= *Marlierea biptera* Amshoff], *Myrcia caesariata* (McVaugh) E. Lucas & C. E. Wilson [= *Marlierea caesariata* McVaugh], *Myrcia cana* (McVaugh) E. Lucas & C. E. Wilson [= *Marlierea cana* McVaugh], *Myrcia caudata* (McVaugh) E. Lucas & C. E. Wilson [= *Marlierea caudata* McVaugh], *Myrcia convexivenia* (B. Holst) E. Lucas & C. E. Wilson [= *Marlierea convexivenia* B. Holst], *Myrcia ensiformis* (McVaugh) E. Lucas & C. E. Wilson [= *Marlierea ensiformis* McVaugh], *Myrcia excoriata* (Mart.) E. Lucas & C. E. Wilson [= *Marlierea excoriata* Mart.], *Myrcia guildingiana* (Griseb.) E. Lucas & C. E. Wilson [= *Psidium guildingianum* Griseb.], *Myrcia insignis* (McVaugh) E. Lucas & C. E. Wilson [= *Marlierea insignis* McVaugh], *Myrcia karuaiensis* (Steyerm.) E. Lucas & C. E. Wilson [= *Aulomyrcia karuaiensis* Steyerm.], *Myrcia ligustrina* (McVaugh) E. Lucas & C. E. Wilson [= *Marlierea ligustrina* McVaugh], *Myrcia lituatinervia* (O. Berg) E. Lucas & C. E. Wilson [= *Myrciaria lituatinervia* O. Berg], *Myrcia maguirei* (McVaugh) E. Lucas & C. E. Wilson [= *Marlierea maguirei* McVaugh], *Myrcia mcvaughii* (B. Holst) E. Lucas & C. E. Wilson [= *Marlierea mcvaughii* B. Holst], *Myrcia multiglomerata* (Amshoff) E. Lucas & C. E. Wilson [= *Marlierea multiglomerata* Amshoff], *Myrcia neuwiedeanae* (O. Berg) E. Lucas & C. E. Wilson [= *Rubachia neuwiedeanae* O. Berg], *Myrcia obversa* (D. Legrand) E. Lucas & C. E. Wilson [= *Marlierea obversa* D. Legrand], *Myrcia pudica* (McVaugh) E. Lucas & C. E. Wilson [= *Marlierea pudica* McVaugh], *Myrcia rugosior* (McVaugh) E. Lucas & C. E. Wilson [= *Marlierea rugosior* McVaugh], *Myrcia scytophylla* (Diels) E. Lucas & C. E. Wilson [= *Marlierea scytophylla* Diels], *Myrcia skortzoviana* (Mattos) E. Lucas & C. E. Wilson [= *Marlierea skortzoviana* Mattos], *Myrcia suborbicularis* (McVaugh) E. Lucas & C. E. Wilson [= *Marlierea suborbicularis* McVaugh], *Myrcia subulata* (McVaugh) E. Lucas & C. E. Wilson [= *Marlierea subulata* McVaugh], *Myrcia sucrei* (G. M. Barroso & Peixoto) E. Lucas & C. E. Wilson [= *Marlierea sucrei* G. M. Barroso & Peixoto], *Myrcia umbraticola* (Kunth) E. Lucas & C. E. Wilson [= *Marlierea umbraticola* (Kunth) O. Berg], *Myrcia uniflora* (McVaugh) E. Lucas & C. E. Wilson [= *Marlierea uniflora* McVaugh], and *Myrcia ventuarensis* (B. Holst) E. Lucas & C. E. Wilson [= *Marlierea ventuarensis* B. Holst]. The following 21 replacement names are created: *Myrcia argentigemma* E. Lucas & C. E. Wilson, *M. aulomyrcioides* E. Lucas & C. E. Wilson, *M. chonodisca* E. Lucas & C. E. Wilson, *M. holstii* E. Lucas & C. E. Wilson, *M. neobuxifolia* E. Lucas & C. E. Wilson, *M. neocuprea* E. Lucas & C. E. Wilson, *M. neodimorpha* E. Lucas & C. E. Wilson, *Myrcia neoestrellensis* E. Lucas & C. E. Wilson, *M. neoglabra* E. Lucas & C. E. Wilson, *M. neoimperfecta* E. Lucas & C. E. Wilson, *M. neomacrophylla* E. Lucas & C. E. Wilson, *M. neomontana* E. Lucas & C. E. Wilson, *M. neoobscura* E. Lucas & C. E. Wilson, *M. neoregeliana* E. Lucas & C. E. Wilson, *M. neoriedeliana* E. Lucas & C. E. Wilson, *M. neoschomburgkiana* E. Lucas & C. E. Wilson, *M. neosuaveolens* E. Lucas & C. E. Wilson, *M. neotomentosa* E. Lucas & C. E. Wilson, *M. neotovarensis* E. Lucas & C. E. Wilson, *M. neovelutina* E. Lucas & C. E. Wilson, and *M. neovorticillaris* E. Lucas & C. E. Wilson. Sixty-four lectotypes are newly designated for the following names: *Aulomyrcia blanchetiana* O. Berg [= *Myrcia blanchetiana* (O. Berg) Mattos], *Aulomyrcia buxifolia* O. Berg [= *Myrcia multiflora* DC.], *Aulomyrcia cambessedeanae* O. Berg [= *Myrcia coelosepala* Kiaersk.], *Aulomyrcia diaphana* O. Berg [= *Myrcia diaphana* (O. Berg) N. Silveira], *Aulomyrcia divaricata* O. Berg [= *Myrcia rufipila* McVaugh], *Aulomyrcia egensis* O. Berg [= *Myrcia egensis* (O. Berg) McVaugh], *Aulomyrcia eumecephylla* O. Berg [= *Myrcia eumecephylla* (O. Berg) Nied.], *Aulomyrcia gigantea* O. Berg [= *Myrcia gigantea* (O. Berg) Nied.], *Aulomyrcia goyazensis* O. Berg [= *Myrcia multiflora* DC.], *Aulomyrcia insularis* (Gardner) O. Berg var. *punctata* O. Berg [= *Myrcia insularis* Gardner], *Aulomyrcia mathewsiana* O. Berg [= *Myrcia mathewsiana* (O. Berg) McVaugh], *Aulomyrcia pallida* O. Berg [= *Myrcia multiflora* DC.], *Aulomyrcia pohliana* O. Berg [= *Myrcia pubiflora* DC.], *Aulomyrcia pyrifolia* (Desv. ex Ham.) O. Berg var. *robusta* O. Berg [= *Myrcia pyrifolia* (Desv. ex Ham.) Nied.], *Aulomyrcia racemosa* O. Berg [= *Myrcia racemosa* (O. Berg) Kiaersk.], *Aulomyrcia rorida* O. Berg [= *Myrcia myrtillifolia* DC.], *Aulomyrcia rostrata* O. Berg [= *Myrcia neorostrata* Sobral], *Aulomyrcia salzmännii* O. Berg [= *Myrcia decorticans* DC.], *Aulomyrcia sphenoides* O. Berg [= *Myrcia sphenoides* (O. Berg) Mattos], *Aulomyrcia*

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stictophylla O. Berg [= *Myrcia stictophylla* (O. Berg) N. Silveira], *Aulomyrcia subobliqua* O. Berg [= *Myrcia subobliqua* (Benth.) Nied.], *Eugenia ferruginea* Poir. [= *Myrcia ferruginea* (Poir.) DC.], *Eugenia micropetala* Mart. [= *Myrcia micropetala* (Mart.) Nied.], *Eugenia quitarensis* Benth. [= *Myrcia quitarensis* (Benth.) Sagot], *Eugeniopsis riedeliana* O. Berg [= *Myrcia neoriedeliana* E. Lucas & C. E. Wilson], *Marlierea cuprea* Amshoff [= *Myrcia neocuprea* E. Lucas & C. E. Wilson], *Marlierea dimorpha* O. Berg [= *Myrcia neodimorpha* E. Lucas & C. E. Wilson], *Marlierea estrellensis* O. Berg [= *Myrcia neoestrellensis* E. Lucas & C. E. Wilson], *Marlierea excoriata* Mart. [= *Myrcia excoriata* (Mart.) E. Lucas & C. E. Wilson], *Marlierea glabra* Cambess. [= *Myrcia neoglabra* E. Lucas & C. E. Wilson], *Marlierea grandifolia* O. Berg [= *Myrcia neoglabra* E. Lucas & C. E. Wilson], *Marlierea macrophylla* Amshoff [= *Myrcia neomacrophylla* E. Lucas & C. E. Wilson], *Marlierea obscura* O. Berg [= *Myrcia neoobscura* E. Lucas & C. E. Wilson], *Marlierea parviflora* O. Berg [= *Myrcia excoriata* (Mart.) E. Lucas & C. E. Wilson], *Marlierea regeliana* O. Berg [= *Myrcia neoregeliana* E. Lucas & C. E. Wilson], *Marlierea regeliana* O. Berg var. *parviflora* Kiaersk. [= *Myrcia neoriedeliana* E. Lucas & C. E. Wilson], *Marlierea schottiana* O. Berg [= *Myrcia neoglabra* E. Lucas & C. E. Wilson], *Marlierea scytophylla* Diels [= *Myrcia scytophylla* (Diels) E. Lucas & C. E. Wilson], *Marlierea suaveolens* Cambess. [= *Myrcia neosuaveolens* E. Lucas & C. E. Wilson], *Marlierea tomentosa* Cambess. [= *Myrcia neotomentosa* E. Lucas & C. E. Wilson], *Marlierea towarensis* O. Berg [= *Myrcia neotovarensis* E. Lucas & C. E. Wilson], *Marlierea verticillaris* O. Berg [= *Myrcia neoverticillaris* E. Lucas & C. E. Wilson], *Myrcia* sect. *Aulomyrcia* Nied., *Myrcia coelosepala* Kiaersk., *Myrcia colpodes* Kiaersk., *Myrcia decorticans* DC., *Myrcia imbricata* Gardner [= *Myrcia racemulosa* DC.], *Myrcia insularis* Gardner, *Myrcia limae* G. M. Barroso & Peixoto [= *Myrcia eumecephylla* (O. Berg) Nied.], *Myrcia littoralis* DC., *Myrcia myrtillifolia* DC., *Myrcia polyantha* DC., *Myrcia pubiflora* DC., *Myrcia pyramidata* O. Berg [= *Myrcia rubiginosa* Cambess.], *Myrcia racemulosa* DC., *Myrcia riodocensis* G. M. Barroso & Peixoto, *Myrcia rubella* Cambess. [= *Myrcia myrtillifolia* DC.], *Myrcia rubiginosa* Cambess., *Myrcia scutulifera* DC. [= *Myrcia racemulosa* DC.], *Myrcia strigipes* Mart. [= *Myrcia neotomentosa* E. Lucas & C. E. Wilson], *Myrciaria ehrenbergiana* O. Berg [= *Myrcia ehrenbergiana* (O. Berg) McVaugh], *Psidium guildingianum* Griseb. [= *Myrcia guildingiana* (Griseb.) E. Lucas & C. E. Wilson], *Rubachia neuwiediana* O. Berg [= *Myrcia neuwiediana* (O. Berg) E. Lucas & C. E. Wilson], and *Rubachia spathulata* O. Berg [= *Myrcia obversa* (D. Legrand) E. Lucas & C. E. Wilson]. A single neotype is designated for *Aulomyrcia ramuliflora* O. Berg [= *Myrcia ramuliflora* (O. Berg) N. Silveira]. Fifteen names are newly synonymized: *Aulomyrcia cambessediana* O. Berg [= *Myrcia coelosepala* Kiaersk.], *Aulomyrcia salzmännii* O. Berg [= *Myrcia decorticans* DC.], *Marlierea regeliana* O. Berg var. *parviflora* Kiaersk. [= *Myrcia neoriedeliana* E. Lucas & C. E. Wilson], *Myrcia amblyphylla* Kiaersk. [= *Myrcia coelosepala* Kiaersk.], *Myrcia dictyophylla* (O. Berg) Mattos & D. Legrand [= *Myrcia myrtillifolia* DC.], *Myrcia heringeriana* Mattos [= *Myrcia multiflora* DC.], *Myrcia limae* G. M. Barroso & Peixoto [= *Myrcia eumecephylla* (O. Berg) Nied.], *Myrcia lucida* McVaugh, *Myrcia lucida* var. *attenuata* McVaugh [= *Myrcia inaequiloba* (DC.) Lemée], *Myrcia lundiana* Kiaersk. [= *Myrcia amazonica* DC.], *Myrcia pallida* (O. Berg) N. Silveira [= *Myrcia multiflora* DC.], *Myrcia parnajibensis* (O. Berg) Kiaersk. [= *Myrcia myrtillifolia* DC.], *Myrcia rorida* (O. Berg) Kiaersk. [= *Myrcia myrtillifolia* DC.], *Myrcia rubella* Cambess. [= *Myrcia myrtillifolia* DC.], and *Myrcia taubatensis* Kiaersk. [= *Myrcia multiflora* DC.].

Key words: *Aulomyrcia*, *Calypttranthes*, Caribbean, Central America, IUCN Red List, *Krugia*, *Marlierea*, *Mozartia*, *Myrcia*, Myrtaceae, South America.

Myrcia DC. s.l. is a large (ca. 750 species; World Checklist of Selected Plant Families [WCSP], 2015), monophyletic group (Lucas et al., 2011) of Neotropical Myrtaceae previously known as subtribe Myrciineae (Berg, 1855–1856; McVaugh, 1968). The group comprises the traditionally accepted genera *Calypttranthes* Sw., *Gomidesia* O. Berg, *Marlierea* Cambess., and *Myrcia* that are paraphyletic or polyphyletic with respect to each other (Lucas et al., 2011; Wilson et al., 2016). *Myrcia* s.l. is an ecologically important genus in the Atlantic forests and cerrado savanna of eastern Brazil and is diverse in other tropical rainforest biomes such as the Amazon and Caribbean (Murray-Smith et al., 2009; Lucas et al., 2011). A monograph of the group is much needed and long overdue and will be supported by a new subgeneric classification (Lucas et al., in prep.). Justification for combining the traditional genera into a more inclusive *Myrcia* was given by Lucas and Sobral (2011); under such a scheme, *Myrcia* s.l. can be divided into morphologically cohesive groups based on the clades of Lucas et al. (2011). One such group corresponds to clade 9 of Lucas et al. (2011), and this

clade is here equated to *Myrcia* sect. *Aulomyrcia* (O. Berg) Griseb.

Most authors have recognized two groups within *Myrcia* s.l. (e.g., de Candolle, 1828; Berg, 1857–1859; Grisebach, 1864; Kiaerskou, 1893). Species with regular calyx lobes not prolonged beyond the ovary and flat hairy disks have been unequivocally referred to a group containing the type species of *Myrcia*, treated under that name at a variety of ranks. In this work we refer to that group as *Myrcia* sect. *Myrcia*. Species with a prolonged hypanthium and with a tendency for the otherwise free calyx lobes to tear at anthesis have been named by the same authors as *Aulomyrcia* O. Berg, also at a variety of ranks. *Aulomyrcia* was initially published as a genus by Otto Berg (1855–1856) and subsequently recognized as a section (Grisebach, 1864; Kiaerskou, 1893; McVaugh, 1968) or subgenus (Niedenzu, 1893; Legrand, 1961) of *Myrcia*. McVaugh (1969) later described a third section, *Myrcia* sect. *Armeriela* McVaugh, in which the calyx and hypanthium are more prolonged than in *Myrcia* sect. *Aulomyrcia*, with a tendency to disintegrate at anthesis. McVaugh

(1969) suggested *Myrcia* sect. *Aulomyrcia* was intermediate between *Myrcia* sections *Myrcia* and *Armeriela*. Infrageneric delimitation of *Myrcia* has always been difficult and unreliable; the taxonomic history of *Myrcia* sect. *Aulomyrcia* is discussed in detail by Lucas et al. (2011). Unpublished data based on whole genome sequencing produced by Lima et al. show clearly that a small number of species with two locules, currently considered synonyms (Sobral et al., 2015) of *M. guianensis* (Aubl.) DC. (not *Myrcia* sect. *Aulomyrcia*), emerge within the *Myrcia* sect. *Aulomyrcia* clade. The necessary transfers of synonymy are made here.

The recent compilation of collaborative checklists, such as the WCSP (2015) and the Lista de Espécies da Flora do Brasil (Sobral et al., 2015), has resulted in considerable taxonomic deflation and the welcomed consensus on the numbers of species in the traditional genera of *Myrcia* s.l. As delimited here, *Myrcia* sect. *Aulomyrcia* is a section of 124 species originally described in *Myrcia* and *Marlierea* and, in one case, *Calyptanthus*. Morphologically, the group is distinguished by a combination of characters such as persistent subfloral or vegetative bracts, an often asymmetrical inflorescence, a tendency toward whorled leaves and terminal inflorescences, (four to five free calyx lobes held erect and away from a uniformly bilocular ovary in flower and fruit, a shortly extended hypanthium that can tear on opening, and usually a slightly convex disk bearing a thin ring of stamens (see Lucas et al., 2011, for further discussion of morphology).

MATERIALS AND METHODS

Taxonomy used herein follows the WCSP (2015) modified where necessary according to the Lista de Espécies da Flora do Brasil (Sobral et al., 2015). Digital images are available at Global Plants (<www.plants.jstor.org>, 2015) or can be made available upon request. Information on the location/deposition of collections or the activities of collectors or authors has been taken from Stafleu and Cowan (1976–1988). Lectotypes are designated where necessary following the International Code of Nomenclature for Algae, Fungi, and Plants (McNeill et al., 2012). Because of difficulties in certainty that a specimen at the institution of an author was the only material examined at the time (McNeill, 2014), lectotypifications are made even when an apparent holotype appears obvious. Unless specified otherwise, selected lectotype material is that most likely used or seen by the protologue author, from the best distributed and representative collection available, usually the top set of the collector. Also unless specified otherwise,

where multiple syntypes are listed by the author, the lectotype gathering is that judged to best match the protologue description. Known isoelectotypes are listed. Remaining syntypes are not listed as they are readily available in protologues available to this study either via the project scratchpad (<http://myrcia.myspecies.info>), which contains images, protologues, and further information, or TROPICOS®. Collections of the following herbaria were visited: BM, BR, G, K, LE, M, NY, P, U, US, W; additional type images from C, F, MO, RB, and S were viewed online (separately from the JSTOR Global Plants website); online access to these collections was via Index Herbariorum (Thiers, 2015). A publication cutoff was necessary to complete this list; species published after 2011, when the main part of this work was carried out, are not treated.

Selected material cited was selected as follows: one specimen from each country and/or state/province except for widespread taxa where one to three species are recorded for each Taxonomic Databases Working Group (TDWG, 2001) level 4 region with emphasis on species records per vegetation type, to a maximum of 20 specimens, to broadly outline the distribution. All selected specimens were seen by one or more authors of this work and are referred to as “known to us.” Ever-expanding websites of specimen records and images, e.g., speciesLink and TROPICOS®, were consulted to ensure species distributions are as accurate as possible. In these cases, only specimens named by an authoritative specialist were used for distribution statements or calculations of extent of occurrence (EOO; IUCN, 2014); with a few noted exceptions, these have not been cited.

Preliminary conservation assessments were made using ArcGIS based on the range parameters of the IUCN (2014) and the protocol of Willis et al. (2003). Early in the assessment process, measurements of area of occurrence (AOO; IUCN, 2014) were discounted in favor of EOO as they consistently over-estimate the level of threat to species with anything other than restricted ranges. Assessments are based on material seen by us, unless specified otherwise where specimen data from the online collections cited above are also used. The category of threat as Vulnerable (VU D2) is used in cases where there is no evidence of a continuing decline or fluctuation in EOO or area or of the extent and/or quality of the habitat (IUCN, 2014) available to a species or whether the species exists in a protected or well-protected area. This lack of evidence is associated with species known from few close locations that have not been subject to recent floristic surveys. Criterion VU D2 allows for this information

gap, suggesting that a species' "small population size and/or restricted distribution make it more prone to the effects of human activities or stochastic events in an uncertain future, and is thus capable of becoming Critically Endangered or even Extinct in a very short time period" (IUCN, 2014: 59). Detailed information regarding environmental threat is from the Encyclopaedia of Earth (EOE, 2015) and the World Database on Protected Areas (WDPA, 2015); extra detail is provided for species associated with McVaugh's (1958) *Marlierea* sect. *Myrciopsis* McVaugh as these were the focus of a separate, unpublished study.

To maintain taxonomic meaning and reduce confusion, we have opted as much as possible to suffix the original epithet with "neo-" where new combinations are made unless this would result in both the epithet and the neo-epithet existing in the same section. All species are bilocular unless specified.

TAXONOMIC CONSPECTUS

Myrcia DC. in Bory de Saint-Vincent, Dict. Class. Hist. Nat. 11: 378. [Jan.] 1827. TYPE: *Myrcia bracteolaris* (Poir.) DC. [= *Myrtus bracteolaris* Poir.] (lectotype, designated by McVaugh [1956a: 143]).

Myrcia sect. **Aulomyrcia** (O. Berg) Griseb., Fl. Brit. W. Ind., 234. 1860. Basionym: *Aulomyrcia* O. Berg, Linnaea 27: 35. 1855. TYPE: *Myrcia multiflora* (Lam.) DC. [= *Eugenia multiflora* Lam.] (lectotype, designated by McVaugh [1956a: 137]).

Krugia Urb., Ber. Deutsch. Bot. Ges. 11: 375. 1893. TYPE: *Krugia elliptica* (Griseb.) Urb. [= *Marlierea elliptica* Griseb.].

Myrcia sect. *Aulomyrcia* Nied., Nat. Pflanzenfam. 3(7): 75–76. 1893, as "Sect. 1. Eu-Aulomyrcia." TYPE: *Myrcia pyrifolia* (Desv. ex Ham.) Nied. [= *Eugenia pyrifolia* Desv. ex Ham., Prodr. Pl. Ind. Occid., 44. 1825], (lectotype, designated here, P-00163115!).

Marlierea Cambess. in A. St.-Hil., Fl. Bras. Mer. 2(20): 373, tab. 156. [3 Aug.] 1833. TYPE: *Marlierea suaveolens* Cambess. (lectotype, designated by McVaugh [1956a: 142]).

Marlierea sect. *Myrciopsis* McVaugh, Mem. New York Bot. Gard. 10: 79. 1958, as *Marlierea* sect. *Myrcioides* McVaugh. [Orthographic error corrected by McVaugh, Fieldiana, Bot. 29(8): 470 1963] TYPE: *Marlierea bipennis* (O. Berg) McVaugh, Fieldiana, Bot. 29: 189. 1956. [= *Myrciaria bipennis* O. Berg, Linnaea 31: 259. 1862].

Myrcia sect. *Armeriela* McVaugh, Taxon 17: 378. 1968. TYPE: *Myrcia inaequiloba* (DC.) Lemée, Fl. Guyane Franç. 3: 150. 1954, non *Myrcia inaequiloba* (DC.) D. Legrand, Atas Simp. Biota Amazônia. 149. 1967 [1968], nom. illeg., isonym. [= *Eugenia inaequiloba* DC., Prodr. [de Candolle] 3: 282. 1828].

Rubachia O. Berg, Linnaea 27: 11. 1855, p.p. (The lectotype species, *Rubachia spiciflora* (Nees & Mart.) O. Berg, designated by McVaugh [1956a: 145] is a species of *Plinia* Plum. ex L. [Sobral, 1995]; the remaining *Rubachia* species are synonyms of *Myrcia* sect. *Aulomyrcia*).

Trees or shrubs; branching usually monopodial. Bracteoles often triangular and acute, usually persistent after fruit fall. Inflorescence of paniculate axes, axillary or emerging from single terminal whorls representing compression of all primary inflorescence nodes, primary axes symmetrical and cymose or asymmetrical and irregularly branched, often with a zigzagged appearance, occasionally reduced and spikelike. Perianth 4- or 5-merous; calyx lobes free to partially or completely fused, irregularly tearing open vertically through the calyx and hypanthial tissue, leaving calyx lobes of markedly different sizes or of regular triangles in a star shape, where tears are deep, staminal scars appear to be at the tips of the calyx lobes; floral disk glabrous; staminal ring thin, comprising less than 40% of total disk width; hypanthium extended in a flared tube beyond the ovary; ovary bilocular, 2 ovules per locule. Fruits globose.

Myrcia sect. *Aulomyrcia* is a distinct but variable, widespread, and speciose clade. Species diversity is highest in the Brazilian northern Atlantic forest and the Amazon, in particular on the Guiana shield. The majority of species in the clade possess inflorescences that are asymmetrical to some degree, often whorled, with persistent, pointed bracts and bilocular flowers with a tendency to tear open vertically, leaving four or five irregular calyx lobes. The clade includes the majority of species accepted in *Marlierea* at the time of writing (ca. 55%) and its traditional synonyms include *Rubachia*, p.p., all bilocular species previously assigned to *Aulomyrcia*, and the ca. 30 species of *Myrcia* sect. *Armeriela*.

Despite encompassing such morphological variety and so many species, coherent subgroups can be recognized in *Myrcia* sect. *Aulomyrcia* that may warrant future formal description. Results from molecular-based studies (e.g., Santos, 2014; Stagge-meier et al., 2015) have been used to supplement the morphological study presented here where five informal species groups are postulated. Ninety-five species are included within these groups, which represent ca. 77% of the 124 species formally considered herein. These may be of interest to those seeking a better understanding of the group for specimen identification and curation but are presented here only as a hypothesis for future testing. It has not been possible to suggest an affiliation for every

species, particularly where no or little material is available for study.

SPECIES GROUP A

This is a group of predominantly low-altitude, moist forest species with unusually long, whorled, wholly terminal inflorescences, coriaceous, often whorled leaves, and a raised or flat midvein; specific examples are *Myrcia insularis* Gardner and *M. clavija* Sobral. These species are most common in the Brazilian Atlantic forests north of Rio de Janeiro, but there are some species endemic to the Amazon forests such as *M. speciosa* (Amshoff) McVaugh.

Included species (15). *Myrcia areolata* (McVaugh) E. Lucas & C. E. Wilson, *M. badia* (O. Berg) N. Silveira, *M. clavija* Sobral, *M. colpodes* Kiaersk., *M. eumecephylla* (O. Berg) Nied., *M. gigantea* (O. Berg) Nied., *M. hexasticha* Kiaersk., *M. insularis* Gardner, *M. liesneri* B. Holst, *M. magna* D. Legrand, *M. neoestrellensis* E. Lucas & C. E. Wilson, *M. obversa* (D. Legrand) E. Lucas & C. E. Wilson, *M. speciosa* (Amshoff) McVaugh, *M. tetraphylla* Sobral, and *M. zetekiana* (Standl.) B. Holst.

SPECIES GROUP B

This group is based on *Marlierea* sect. *Myrciopsis* McVaugh who referred it to *Marlierea* rather than to *Myrcia* because of the nearly closed buds, presence of dibrachiate hairs, and the cymose tendency of the lateral inflorescence, often with flattened and/or winged rachises; McVaugh (1958) also noted that winged branchlets were characteristic of the group. We extend the group's circumscription to include all those species with cymose inflorescences and flattened rachises, regardless of the position of the inflorescence and also to those convincingly affiliated to those species in cited works. In this way, the group is superficially similar to species that emerge in clade 7 of Lucas et al. (2011); species of that group differ in having turbinate hypanthia with calyx lobes that do not tear below the staminal ring, vegetative growth that is often sympodial, and very precisely opposite branching within the cyme. Species of group B usually have an extended but flared hypanthium with calyx lobes that tear into the staminal ring, monopodial growth, and subopposite to alternate branching within the cyme.

Included species (31). *Myrcia bipennis* (O. Berg) McVaugh, *M. biptera* (Amshoff) E. Lucas & C. E. Wilson, *M. bolivarensis* (Steyerm.) McVaugh, *M. caesariata* (McVaugh) E. Lucas & C. E. Wilson, *M. calcicola* Proctor, *M. cana* (McVaugh) E. Lucas & C. E. Wilson, *M. caudata* (McVaugh) E. Lucas & C. E.

Wilson, *M. chonodisca* E. Lucas & C. E. Wilson, *M. compta* McVaugh, *M. convexivenia* (B. Holst) E. Lucas & C. E. Wilson, *M. ensiformis* (McVaugh) E. Lucas & C. E. Wilson, *M. ferruginea* (Poir.) DC., *M. gentryi* B. Holst, *M. guildingiana* (Griseb.) E. Lucas & C. E. Wilson, *M. induta* McVaugh, *M. karuaiensis* (Steyerm.) E. Lucas & C. E. Wilson, *M. kylistophylla* B. Holst, *M. lituatinervia* (O. Berg) E. Lucas & C. E. Wilson, *M. maguirei* (McVaugh) E. Lucas & C. E. Wilson, *M. mcvaughii* (B. Holst) E. Lucas & C. E. Wilson, *M. minutiflora* Sagot, *M. multiglomerata* (Amshoff) E. Lucas & C. E. Wilson, *M. neoschomburgkiana* E. Lucas & C. E. Wilson, *M. neotovarensis* E. Lucas & C. E. Wilson, *M. portoricensis* (Britton) Cedeño-Mald. & Breckon ex F. S. Axelrod, *M. pudica* (McVaugh) E. Lucas & C. E. Wilson, *M. rotundata* (Amshoff) McVaugh, *M. sessiliflora* McVaugh, *M. skeldingii* Proctor, *M. suborbicularis* (McVaugh) E. Lucas & C. E. Wilson, and *M. ventuarensis* (B. Holst) E. Lucas & C. E. Wilson.

SPECIES GROUP C

This includes the decorticans complex (Holst, 2002; Holst & Kawasaki, 2004) distinguished by reddish brown hairs turning gray with age, petioles often corky or flaky, four or five internally pubescent and unequally tearing calyx lobes, persistent inflorescence bracts, and cotyledons somewhat fused or indistinct. Specific examples are *Myrcia inaequiloba*, *M. saxatilis* (Amshoff) McVaugh, and *M. umbraticola* (Kunth) E. Lucas & C. E. Wilson. This group also contains *M. aulomyrcioides* E. Lucas & C. E. Wilson, a new name (\equiv *Calyptranthes multiflora* Poepp. ex O. Berg), the single species of *Calyptranthes* that so far emerges with species of *Myrcia* sect. *Aulomyrcia* in molecular analysis (Wilson et al., 2016); there is also clear support (Staggemeier et al., 2015) that *M. multiflora* and *M. racemosa* (O. Berg) Kiaersk. are associated with this group as well as species (Lima et al., in prep.) formerly included as synonyms of *M. guianensis* (not *Myrcia* sect. *Aulomyrcia*) such as *M. littoralis* DC. and *M. myrtillifolia* DC.

Included species (33). *Myrcia albidotomentosa* (Amshoff) McVaugh, *M. antillana* McVaugh, *M. aulomyrcioides* E. Lucas & C. E. Wilson, *M. blanchetiana* (O. Berg) Mattos, *M. coelosepala* Kiaersk., *M. decorticans* DC., *M. diaphana* (O. Berg) N. Silveira, *M. dichrophylla* D. Legrand, *M. egensis* (O. Berg) McVaugh, *M. exploratoris* McVaugh, *M. fusca* B. Holst & M. L. Kavas., *M. grandis* McVaugh, *M. inaequiloba* (DC.) D. Legrand, *M. littoralis* DC., *M. matthewsiana* (O. Berg) McVaugh, *M. micropetala* (Mart.) Nied., *M. morroqueimadensis* Kiaersk., *M.*

multiflora (Lam.) DC., *M. myrtillifolia* DC., *M. neocuprea* E. Lucas & C. E. Wilson, *M. platyclada* DC., *M. polyantha* DC., *M. porphyrea* McVaugh, *M. pubiflora* DC., *M. quitarensis* (Benth.) Sagot, *M. racemosa* (O. Berg) Kiaersk, *M. racemulosa* DC., *M. ramuliflora* (O. Berg) N. Silveira, *M. rufipila* McVaugh, *M. rupta* M. L. Kawas. & B. Holst, *M. saxatilis* (Amshoff) McVaugh, *M. scytophylla* (Diels) E. Lucas & C. E. Wilson, *M. subobliqua* (O. Berg) Nied., and *M. umbraticola* (Kunth) E. Lucas & C. E. Wilson.

SPECIES GROUP D

A fourth group of species is associated with the widespread species *Myrcia amazonica* DC. In their reddish or sordid indumenta and impressed midveins these species resemble those of the decorticans complex (Holst, 2002; Holst & Kawasaki, 2004). The arrangement distinguishing these two groups was followed in light of authors (such as McVaugh, 1969; Kawasaki & Holst, 1994; Holst & Kawasaki, 2004) who cite the presence of five internally glabrous calyx lobes that are “usually about the same size” (McVaugh, 1969: 110) as indicative of an indepen-

dent origin for these species. The petioles of *M. amazonica* and related species are never corky.
Included species (6). *Myrcia amazonica* DC., *M. pyrifolia* (Desv. ex Ham.) Nied., *M. riococensis* G. M. Barroso & Peixoto, *M. rubiginosa* Cambess., *M. salticola* (Steyerm.) McVaugh, and *M. santateresana* Sobral.

SPECIES GROUP E

This includes species with partially or wholly fused buds that tear deeply through the hypanthium and disk at anthesis into regular star-shaped flowers, often with staminal scars remaining only on the tips of the remaining calyx lobes.
Included species (10). *Myrcia neodimorpha* E. Lucas & C. E. Wilson, *M. neoglabra* E. Lucas & C. E. Wilson, *M. neoobscura* E. Lucas & C. E. Wilson, *M. neoregeliana* E. Lucas & C. E. Wilson, *M. neoriedeliana* E. Lucas & C. E. Wilson, *M. neo-suaveolens* E. Lucas & C. E. Wilson, *M. neotomentosa* E. Lucas & C. E. Wilson, *M. newwiedeana* (O. Berg) E. Lucas & C. E. Wilson, *M. rugosior* (McVaugh) E. Lucas & C. E. Wilson, and *M. sucrei* (G. M. Barroso & Peixoto) E. Lucas & C. E. Wilson.

KEY TO INFORMAL SPECIES GROUPS IN MYRCIA SECT. AULOMYRCIA

This key may be used to roughly sort specimens or to help narrow down an identification. It is emphasized, however, that the key is intended primarily to present useful diagnostic suites of characters while the evolutionary relationships and groupings of species remain untested and informal concepts.

- 1. Inflorescence of long, terminal, asymmetrical panicles, often whorled or in decussate pairs subtended by prominent decussate bracts; midvein flat or raised species group A
- 1'. Inflorescence otherwise not whorled or decussate; midvein usually flat or impressed; bracts below inflorescence not prominent 2
- 2. Inflorescence of lateral or terminal, cymose panicles, often in clusters, rachises often flattened and/or winged species group B
- 2'. Inflorescence of terminal and subterminal, asymmetrical panicles, rachises rarely flattened 3
- 3. On anthesis, calyx tearing through hypanthium and disk, leaving a 5-parted, star-shaped structure .. species group E
- 3'. On anthesis, calyx tearing to hypanthium rim only, leaving 4 to 5 regular or irregular calyx lobes 4
- 4. Four to five internally pubescent calyx lobes, sometimes of irregular sizes; petioles often corky ... species group C
- 4'. Five internally glabrous or at most strigose calyx lobes of roughly equal size; petioles never corky .. species group D

1. *Myrcia abbotiana* (Urb.) Alain, Mem. New York Bot. Gard. 21(2): 138. 1971. Basionym: *Eugenia abbotiana* Urb., Repert. Spec. Nov. Regni Veg. 20: 341. 1924. *Mozartia abbottiana* (Urb.) Urb., Ark. Bot. 22: 24. 1929. TYPE: [Dominican Republic] Santo Domingo. “adolum austalem sinus samanensis prope sinum San Lorenzo,” Apr., sine anno, *W. L. Abbot* 2243 (holotype, US not seen). [No species group assignment].

Habitat and distribution. *Myrcia abbotiana* is endemic to the Dominican Republic on serpentine soils between altitudes of 10 and 400 m.

IUCN Red List category. *Myrcia abbotiana* has an EOO of ca. 500 km² and occurs in two main areas over three districts. One population exists near the capital city Santo Domingo with no environmental protection in an area surrounded by agricultural expansion; the other exists on and around the Samaná Peninsula, at least some of which is protected in the Parque Nacional Los Haitises. The species is well represented in local (JSBD) and international herbaria, suggesting reasonable population size and occupation of more than five distinct localities. We, therefore, list this species as Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia abbotiana* was placed by Urban into a segregate genus, *Mozartia* Urb., on the basis of the character of a single locule within the ovary. The study of Santos (2014) demonstrates this species to emerge within *Myrcia* sect. *Aulomyrcia*.

Selected specimens. DOMINICAN REPUBLIC. **Distrito Nacional:** vacacional Matua, on the curve of the river Matua next to the “balneario,” *Lucas 1108* (K). **Hato Mayor:** Sabana de La Mar Parque Nacional Los Haitises, Bahia San Lorenzo, despues de la Cueva de Linea, yendo hacia Los Naranjos, *Clase 7311* (K). **Samaná:** Península de Samaná Laguna, slope of Pan de Azucar, *Ekman 15178* (K).

2. *Myrcia albidotomentosa* (Amshoff) McVaugh, Mem. New York Bot. Gard. 18: 79. 1969. Basionym: *Aulomyrcia albidotomentosa* Amshoff, Bull. Torrey Bot. Club 75: 532. 1948. TYPE: British Guiana. Kaieteur savanna, 6 Sep. 1937, *C. I. Sandwith 1392* (holotype, K-000342548!; isotypes, NY!, U-0102924!, US!). [Species group C].

Habitat and distribution. *Myrcia albidotomentosa* is found from northern South America to northern Brazil, reported from an altitude of 360 m.

IUCN Red List category. *Myrcia albidotomentosa* has an EOO of ca. 320,000 km² and has been collected in multiple ecoregions (WWF, 2014), several of which are under relatively low levels of threat (EOE, 2015). This species is of Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia albidotomentosa* has a somewhat thickened staminal ring bearing white hairs. Its placement in *Myrcia* sect. *Aulomyrcia* is evident from the tetramerous flowers, corky petioles, and the asymmetric inflorescence architecture with filiform bracts subtending each flower. The species has white silky hairs covering the hypanthium and calyx lobes that are lightly hairy internally; the slightly thickened discolorous leaves with impressed venation are reminiscent of *M. inaequiloba*. Holst (2002) provided further description and discussion and noted similarity in the coriaceous, dry, reddish brown leaves and short, corky-rimose petioles with species of the decorticans complex; additional specimens are also cited in that work.

Selected specimens. BRAZIL. **Amazonas:** encosta da serra Aracá, *N. A. Rosa 2371* (NY). GUYANA. **Potaro-Siparuni:** Mure-mure creek to ca. 3 mi. above mouth, beyond Mure-mure savanna, *Cowan 2200* (K). SURINAME. **Sipaliwini:** Tafelberg Mtn., *Maguire 24734* (K). VENEZUELA. **Amazonas:** Atures, Río Coro-Coro, W of Serranía de Yutaje, *Holst 3102* (K). **Bolívar:** Heres, Cerro Marutani,

cumbre, afloramiento de piedra arenisca en la altiplanicie a lo largo del río Carla, afluente de las cabeceras del río Paragúa, *Steiermark 124087* (NY).

3. *Myrcia amapensis* McVaugh, Mem. New York Bot. Gard. 18: 80. 1969. TYPE: Brazil. Amapá: coastal region, Km. 134, Agua Azul, rd. to Amapá, 23 July 1962, *J. M. Pires 52247* (holotype, MICH-1109489!; isotypes, NY-00405379!, US-00117733!, VEN-76830!). [No species group assignment].

Habitat and distribution. *Myrcia amapensis* is found in coastal and riverine regions of northern Brazil, including Amapá, Para, and Amazonas at an altitude not exceeding ca. 5 m.

IUCN Red List category. Authoritatively named specimens of *Myrcia amapensis*, available online (speciesLink, 2015; TROPICOS®, 2015), report that this species has also been collected in the Ducke Reserve near Manaus, Brazil. This gives the species an EOO of ca. 40,000 km², disqualifying it from a category of threat (IUCN, 2014). However, the species is known from less than five collections, and more information regarding its abundance is required before a category of threat can be assigned. It is assessed as Data Deficient (DD) according to IUCN criteria (2014).

Notes. Only the type and one other collection of *Myrcia amapensis* have been seen for this study. This species strongly resembles *M. multiflora* in both leaf and floral morphology. In *M. amapensis*, the dried leaves are browner than would be expected in *M. multiflora*, and there is a tendency for subsessile leaves.

Selected specimen. BRAZIL. **Pará:** Almeirim, Mt. Dourado, área da agua azul, prox. gleba angelim da reserva genética, *Pires 1382* (NY).

4. *Myrcia amazonica* DC., Prodr. [de Candolle] 3: 250. 1828. *Aulomyrcia amazonica* (DC.) O. Berg, Linnaea 27: 41. 1855. TYPE: Brazil. Amazonas: Solimões, s.d., *C. F. P. Martius s.n.* (lectotype, designated by McVaugh [1969: 110], M-0136802!; isolectotypes, G-DC!, M-0136800!). [Species group D].

Myrcia lundiana Kiaersk., Enum. Myrt. Bras., 78. 1893, replacement name. Replaced name: *Aulomyrcia vautheriana* O. Berg in Linnaea 30: 655. 1861, syn. nov. TYPE: [Brazil.] Brasilia, s.d., *herb. Richard s.n.* (holotype, P-00161048!).

Habitat and distribution. *Myrcia amazonica* is widespread throughout tropical America from moist forests at altitudes from ca. 50 to 1000 m.

IUCN Red List category. The EOO of *Myrcia amazonica* exceeds 5 million km² and is a very commonly collected species from forest habitats. *Myrcia amazonica* is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia amazonica* has relatively small (no more than ca. 2 mm) flowers for *Myrcia* sect. *Aulomyrcia*, five regularly sized and internally glabrous (or at most strigose) calyx lobes, and flat to impressed midveins. *Myrcia lundiana* is cited by Sobral et al. (2015) as occurring in Espírito Santo and Rio de Janeiro. The type collection is recognizable as *M. amazonica*, in particular sharing the large inflorescence with very small flowers, leaf shape, and venation.

Selected specimens. BELIZE. Toledo Distr., near San Antonio, *Gentle* 7512 (K). BOLIVIA. **Santa Cruz:** Velasco, Parque Nac. Noel Kempff M. Camp. Huanchaca, *Killeen* 7500 (K). BRAZIL. **Acre:** Rio Yaco, near mouth of Rio Macauhan (tributary of Rio Yaco), *Krukoff* 5705 (K). **Amapá:** Rio Falsino, ca. 10 km upstream of confluence with Rio Araguari, W bank, *Rabelo* 2377 (K). **Amazonas:** Ponta Negra, banks of Rio Negro, *Prance* 4841 (K); ca. 90 km N of Manaus, Distr. Agropec. Suframa, rod. BR 174, Km. 72, faz. Dimona, *Nee* 42957 (K). **Bahia:** Estr. entre Sururu e Vila Brazil, a 6–14 km de Sururu, a 12 km de Buerarema, *Mori* 12877 (K); 6 km N of Barra da Estiva, not far from Rio Preto, *Harley* 15646 (K); arredores de Catolés, *Harley* 50330 (K); Abaíra, Agua Limpa, *Ganev* 2585 (K). **Distrito Federal:** Brasília, Rod. Belém–Brasília, *Kuhlmann* 287 (K). **Espírito Santo:** Linhares, Res. Nat. Vale, *Folli* 6250 (K). **Goiás:** Araguaína, Belém–Brasília, *Prance* 58988 (K). **Mato Grosso:** Barra do Garças, Xavantina Rd., 77 km from Barra do Garças, *Hunt* 6007 (K); margin of Garapu airstrip, *Prance* 59190 (K). **Minas Gerais:** Distr. Santana do Rio Petro (Cabeça de Boi), APA do Parque Nac. Serra do Cipó, *Santos* 353 (K). **Pará:** Oriximiná, Cachoeira Porteira, porto do Índio, *Ferreira* 9627 (K). **Rio de Janeiro:** Macaé, Estr. para Carepebus, Faz. Jurubatiba, *de Lima* 2898 (K). **Rondônia:** Costa Marques, Chapada dos Parecis, Distr. Alta Floresta, estr. P-56, Km. 17, *Cid* 4539 (K). **Roraima:** Boa Vista, Serra de Tepequém, *Silva* 394 (K). **Santa Catarina:** Horto florestal, I.N.P., *Reitz* 3116 (K). COSTA RICA. **Puntarenas:** Parque Nac. Corcovado Sirena, bank of Rio Claro, *Delprete* 5171 (K). DOMINICA. Syndicate Estate, *Pendry* 307 (K). DOMINICAN REPUBLIC. Cordillera Central, *Ekman* 6355 (K). FRENCH GUIANA. Pic Matecho versant sud, *Granville* 14303 (K). GUYANA. **East Berbice-Corentyne:** Arabupu, s. coll. 48 (K); Demerara-Mahaica, along Linden–Soesdyke Hwy., 16 mi. S of Georgetown, W of Swan Settlement, *Pipoly* 9148 (K). HAITI. Massif de la Hotte, western group, Tiburon, Morne Citadelle, *Ekman* 10543 (IJ). PUERTO RICO. Caribbean Nat. Forest, along Quebrada Sonadora, downstream from rte. 186 to jct. Rio Espírito Santo, *Axelrod* 4402 (K). ST. VINCENT. s. loc., *Resil* 181 (K). SURINAME. **Brokopondo:** Van Bloommesteijn Lake, Tonka Island, emplacement, near guesthouse, *Bhikhi* 681 (K). TRINIDAD AND TOBAGO. St. Andrew, Arena

Reserve, *Broadway* s.n. (K). VENEZUELA. **Bolívar:** 1–4 km N of El Pauji on trail to Uaipaur, *Liesner* 19488 (K).

5. *Myrcia antillana* McVaugh, J. Arnold Arbor. 54: 311. 1973. TYPE: Lesser Antilles. St. Lucia: Savanne Edmund Distr., SE of Piton Troumassée, 11–12 May 1958, *G. R. Proctor* 17973 (holotype, MICH-1109487!; isotypes, A-00071062!, IJ!, US-00117734!). [Species group C].

Habitat and distribution. *Myrcia antillana* has been collected from the Lesser Antilles, from altitudes of 150–850 m.

IUCN Red List category. *Myrcia antillana* is known to us from three collections, well spread amongst the islands of the Lesser Antilles. Herbarium collections from the region are not readily available online or otherwise, making it hard to estimate the frequency of this species in this region; however, it is represented by six separate gatherings at the Institute of Jamaica. *Myrcia antillana* appears restricted to the Lesser Antilles, with an EOO of > 1000 km² and a correspondingly small AOO due to its restriction to the islands. The islands themselves suffer from land alteration associated with mining, agriculture, population increase, and tourism. *Myrcia antillana* is assessed here as Endangered (EN) according to IUCN criteria (2014).

Notes. *Myrcia antillana* resembles *M. decorticans* in having an impressed midvein, a terminal inflorescence covered in rusty hairs comprising two long, sturdy panicles, corky petioles, and free calyx lobes that tear on opening. The former species is larger and thicker in every respect. The leaves of *M. antillana* have a mottled, shiny appearance.

Selected specimens. DOMINICA. **Saint Joseph:** Layou, Layou Forest, Belle Montagne, *Ramage* s.n. (K). GUADELOUPE. s. loc., *Barrier* 2400 (NY). ST. LUCIA. **Savanne Edmund:** SE of Piton Troumassée, *Proctor* 17733 (IJ). ST. VINCENT. Mt. Grande Bonhomme, *Proctor* 26063 (IJ).

6. *Myrcia argentigemma* E. Lucas & C. E. Wilson, nom. nov. Replaced name: *Marlierea spruceana* O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14: 34. 1857, non *Myrcia spruceana* O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14(1): 165. 1857. TYPE: [Brazil. Amazonas:] Rio Negro, inter Barra et Barcellos, s.d., *R. Spruce* 1905 (holotype, M-0171095!; isotypes, GOET-008240!, K-000330459!, K-000330460!,

MICH-1109462!). [No species group assignment].

Habitat and distribution. *Myrcia argentigemma* is found in dense Amazonian forest, on sandy soils, riverbanks, and igapó forest in Venezuela, Colombia, Peru, and Brazil at altitudes of ca. 100–200 m.

IUCN Red List category. *Myrcia argentigemma* is a well-collected, widespread species known to us from more than 15 independent localities and is well represented in online herbaria (EOO > 300,000 km²). *Myrcia argentigemma* is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia argentigemma* is a species that is distinguished by an impressed midvein on the adaxial blade surface; monopodial branching; a terminal, cymose inflorescence; and turbinate, closed buds that are covered with silver-colored appressed hairs.

Selected specimens. BOLIVIA. Pando, Rio Abuna, *Prance* 8512 (K). BRAZIL. **Acre:** Serra da Moa, *Prance* 12264 (K). **Amazonas:** Manaus, Cachoeira alta Tarumã, *Prance* 2686 (K). **Mato Grosso:** Rio Aripuanã, rd. from Núcleo Pioneiro de Humboldt to New Airport, *Berg* 19857 (K). **Rondônia:** Espigão de Oeste, Rod. Cuiabá–Porto Velho, *Cid* 4670 (K). COLOMBIA. **Vaupés:** Mitu & vic., *Zarucchi* 1831 (K).

7. *Myrcia areolata* (McVaugh) E. Lucas & C. E. Wilson, comb. nov. *Marlierea areolata* McVaugh, *Fieldiana, Bot.* 29: 175. 1956. TYPE: Peru. Loreto: Middle Ucalayli, 1923, *G. Tessmann* 3264 (holotype, G-00223340!; isotypes, F-0040039F!, NY-00038434!, S-052556!, US-00153783!). [Species group A].

Habitat and distribution. *Myrcia areolata* is found in the forests of northern Peru at altitudes of ca. 100–220 m.

IUCN Red List category. *Myrcia areolata* has been assessed by Bocángel et al. (2006) to be Endangered (EN) according to IUCN criteria (2014).

Notes. *Myrcia areolata* resembles *M. amazonica* but has a raised midvein. McVaugh (1969) also mentions the terminal inflorescence of this species. *Myrcia areolata* has terminal, whorled inflorescences; flowers with four, fairly regular, internally glabrous calyx lobes; and decorticating bark on the rachises. No specimens of this species could be located in visited herbaria or online; this suggests a rare species or extremely narrow distribution.

8. *Myrcia aulomyrcioides* E. Lucas & C. E. Wilson, nom. nov. Replaced name: *Calyptranthes multiflora* Poepp. ex O. Berg in C. F. P. von Martius & auct. suc. (eds.), *Fl. Bras.* 14: 42. 1857, non *Myrcia multiflora* (Lam.) DC., *Prodr.* [de Candolle] 3: 244. 1828. *Chytraculia multiflora* (Poepp. ex O. Berg) Kuntze, *Revis. Gen. Pl.* 1: 238. 1891. TYPE: [Brazil.] Amazonas: Solimões, flumen Teffe, 1834, *E. F. Poeppig* 2684 (lectotype, designated by Araújo & Lucas [2013: 386], W-0028208!; isotypes, F-0064856F!, F-0064857F!, G-00227471!, G-00227472!, HAL-0089621!, M not seen, MICH-1109778!, NY-00386766!, P-00723209!, W-0031794!). [Species group C].

Habitat and distribution. *Myrcia aulomyrcioides* is found in mixed flat lowland to montane forest on riverbanks, sand, and clay. It is widespread in Amazonian biomes from Venezuela to Bolivia and Brazil at altitudes of ca. 0–800 m.

IUCN Red List category. *Myrcia aulomyrcioides* is recorded from multiple localities (speciesLink, 2015), has an EOO of ca. 340,000 km², and occurs in several ecoregions (WWF, 2015), some under relatively low levels of threat (EOE, 2015). *Myrcia aulomyrcioides* is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. Wilson et al. (2016) reported *Myrcia aulomyrcioides*, previously recognized as *Calyptranthes*, to emerge in a molecular-based phylogeny with other species of *Myrcia* sect. *Aulomyrcia*. Morphologically, the species resembles *M. caesariata* and *M. biptera* in its possession of mixed terminal and lateral bunches of glabrous, cymose panicles with flattened rachises. Holst (2002) provided more description, discussion, and specimen citations; he also observes that buds in collections from the Lesser Antilles open by longitudinal tearing. In the same work, Holst suggested that *C. forsteri* O. Berg could just as well be placed in *Marlierea*; further work is required to assess relationships between these species.

Selected specimens. BOLIVIA. **Pando:** 74 km SW Cobija, Puerto Oro, *Pennington* 153 (K). BRAZIL. **Amazonas:** Vila Bittencourt, *do Amarel* 575 (K). **Rondônia:** Rio Pacaás Novos, 8–25 km, above mouth, *Prance* 6827 (K). **Roraima:** Rorainópolis, Res. Pop. Xixuaú–Xiparina, *Araújo* 1884 (K). COLOMBIA. **Vichada:** Parque Nac. El Tuparro, along Cano Peinilla, *Zarucchi* 3631 (K). PERU. **Loreto:** Maynas, Pebas, Quebrada “tuny,” margen derecha del Rio Ampiyacu, *Revilla* 564 (G). VENEZUELA. **Amazonas:** San Carlos de Rio Negro, entre San Carlos de Rio Negro y la boca del Rio Casiquare, *Stergios* 13092 (US).

9. *Myrcia badia* (O. Berg) N. Silveira, Roessleria 7: 66. 1985. *Aulomyrcia badia* O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14: 547. 1859. TYPE: [Brazil.] Brasilia, s.d., *L. Riedel s.n.* (holotype, LE-00007023!). [Species group A].

Habitat and distribution. Insufficient material is available to provide a meaningful distribution for *Myrcia badia*.

IUCN Red List category. *Myrcia badia* is known only from the type from an unspecified locality in Brazil. As such, the species is assessed as Data Deficient (DD) according to IUCN criteria (2014).

Notes. The type specimen of *Myrcia badia* has a flat to channeled midvein and a terminal to subterminal pair of long, glabrous panicles and deciduous bracts. Bracts that are large (to 2.5 cm), foliose, and lightly pubescent subtend the secondary branches of the inflorescence. The combined characters of thick, long leaves drying brown and the terminal, whorled inflorescence with bracts suggest an affinity with species from the littoral coasts of Brazil (and a few from the Amazon basin/Amazonia), only a few of which (e.g., *Myrcia subulata* (McVaugh) E. Lucas & C. E. Wilson) do not have a raised midvein.

10. *Myrcia bipennis* (O. Berg) McVaugh, Fieldiana, Bot. 29: 189. 1956. Basionym: *Myrciaria bipennis* O. Berg, Linnaea 31: 259. 1862. *Marlierea bipennis* (O. Berg) McVaugh, Mem. New York Bot. Gard. 10: 79. 1958. TYPE: Brazil. Rio Negro, Dec. 1854, *R. Spruce* 3770 (holotype, BR-0000008259134!; isotypes, BM-000953636!, F-0093423F!, G-00227912!, K-000330540!, K-000330541!, K-000330542!, MICH-1109536!, NY-00405289!, P-00217954!, P-00217953!). [Species group B].

Habitat and distribution. *Myrcia bipennis* is found in the forests of Northern Brazil (Amazonas and Acre), Guyana, and Venezuela (Amazonas), from an altitude of ca. 100 m.

IUCN Red List category. *Myrcia bipennis* is known from nine collections from seven localities, with an EOO > 600,000 km². The species is recorded from largely intact areas in which human encroachment has just begun (Iquitos varzeá; WWF, 2015). However, the region is threatened by logging, gold mining, deforestation for agricultural expansion, and oil extraction (EOE, 2015). Should habitat

removal persist, the conservation status would need to be reviewed. At present, the species is assessed as Least Concern (LC) according to IUCN (2014) criteria.

Notes. *Myrcia bipennis* is the type species of McVaugh's (1958) *Marlierea* sect. *Myrciopsis*; there is a clear resemblance to other species in this group such as *Myrcia neoschomburgkiana* and *M. biptera*. *Myrcia bipennis* is entirely glabrous with subsessile, or very shortly petiolate, leaves with a convex midvein; internodes are lightly or very distinctly winged. The inflorescence is in bunched, lateral panicles with flattened rachises; fruits are globose with persistent, short, irregular calyx lobes.

Selected specimens. BRAZIL. **Acre:** Porto Valter, *Maas* 13194 (NY). **Amazonas:** cachoeira Caranguejo, Rio Cauabury, *Holt* 551 (NY). GUYANA. **Barima-Waini:** Arukamai River, Aruka River, *Forest Department of British Guiana* 924 (K).

11. *Myrcia biptera* (Amshoff) E. Lucas & C. E. Wilson, comb. nov. Basionym: *Marlierea biptera* Amshoff, Recueil Trav. Bot. Néerl. 42: 3. 1950. TYPE: Suriname. Gonini River, 20 Feb. 1918, *B. W. [J. W. Goggrijp]* 3719 (holotype, U-0049625!; isotype, NY-00405288!). [Species group B].

Habitat and distribution. *Myrcia biptera* has been collected from riverine sites in Surinam; the altitude of these collections is not precisely known.

IUCN Red List category. *Myrcia biptera* is known only from the type collection and from a relatively poorly known and collected area. An EOO cannot be calculated, and we consider the species to be rare. The single known collection is from the Guianan moist forests, where environmental threat is low, protected areas are few, and conservation strategies are required (WWF, 2015). This species was last collected in 1950. The area in which the specimens were collected still appears to be intact (Google Inc., 2015) but is not protected. The rarity of the species and this lack of protection make it vulnerable to stochastic change. *Myrcia biptera* is assessed as Vulnerable (VU D2) according to IUCN criteria (2014).

Notes. *Myrcia biptera* is a species distinguished by branchlet internodes bearing wings alternating in orientation, long-acuminate leaves (to 25 cm) with convex midveins, and mixed terminal and lateral bunches of glabrous, cymose panicles with flattened

rachises; the calyx tears very irregularly at anthesis, often leaving a single, much larger calyx lobe.

12. *Myrcia blanchetiana* (O. Berg) Mattos, Arq. Bot. Estado São Paulo 4: 59. 1966. Basionym: *Aulomyrcia blanchetiana* O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14: 65. 1857. TYPE: [Brazil.] Bahia, *J. S. Blanchet 3391* (holotype, B†; lectotype, designated here, P-00161509!; isoelectotypes, BM-000953637!, BR-0000005238330!, C-10015829!, F-0064685F!, F-0064686F!, G-00222508!, HAL-0089798!, K-000343975!, MICH-1109842!, NY-00386648!, NY-00386649!, NY-00386650!, P-00161510!, P-00751186). [Species group C].

Habitat and distribution. *Myrcia blanchetiana* has been collected in Bahia from campo rupestre, caatinga, and sandy soils from altitudes of 500–1800 m.

IUCN Red List category. *Myrcia blanchetiana* is a commonly collected species with an EOO > 90,000 km². *Myrcia blanchetiana* is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia blanchetiana* is a distinctive species without bracts and with a short inflorescence no more than ca. 5.5 mm; fruits are uniform small balls with regular, persistent calyx lobes. Unconfirmed identifications (speciesLink, 2015) suggest this species may occur in Minas Gerais and Pernambuco in Brazil.

Selected specimen. BRAZIL. **Bahia:** Mucugê, Pico do Gobria, *Castro 107620* (K).

13. *Myrcia bolivarensis* (Steyerm.) McVaugh, Mem. New York Bot. Gard. 18: 81. 1969. Basionym: *Aulomyrcia bolivarensis* Steyerm., Fieldiana, Bot. 28: 1004. 1957. TYPE: [Venezuela.] Bolívar: Patari-tepui, 30 Oct. 1944, *J. A. Steyermark 59534* (holotype, F-0064687F!; isotypes, F-0064687F!, NY-00386644!, U-0005098!, US-00048595!, VEN-37418!). [Species group B].

Habitat and distribution. *Myrcia bolivarensis* is a montane species found on slopes overlying sandstone from Venezuela to Guyana and from altitudes of ca. 1800–2100 m.

IUCN Red List category. *Myrcia bolivarensis* is known from 18 collections from 16 sites; it is well protected, with 14 out of 18 collections made in

protected areas (WDPA, 2015). The last known collection was made in 2008 (*Meier 14839*, K!). *Myrcia bolivarensis* is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. The protologue of *Myrcia bolivarensis* compares the species to *M. neoschomburgkiana*, and McVaugh (1969) noted a resemblance to *M. minutiflora*. *Myrcia bolivarensis* has strongly acuminate leaves and bunches of reduced lateral inflorescences with silky pubescence, resembling these species and also *M. caudata*. Therefore, the species may be compared to those of McVaugh's (1958) *Marlierea* sect. *Myrciopsis*. Fruits strongly resemble the smooth dark balls of *M. caudata* but with unusually tiny remnants of the hypanthium/calyx lobes. A further difference from *M. caudata* can be seen in the midvein, convex in *M. bolivarensis* (vs. clearly raised in *M. caudata*).

Selected specimens. GUYANA. **Cuyuni-Mazaruni:** 2–5 km NW of N prov. of Roraima, *Hahn 5473* (NY). **Potaro-Siparuni:** Mt. Ayanganna, E face, plateau above 2nd of 4 escarpments, *Clarke 9289* (K). VENEZUELA. **Amazonas:** Atures, Cumbre del Cerro Yavi, Rio Parucito, *Huber 11851* (K). **Bolívar:** St. Teresita de Kavanayén, *Steyermark 60435* (NY, U).

14. *Myrcia caesariata* (McVaugh) E. Lucas & C. E. Wilson, comb. nov. Basionym: *Marlierea caesariata* McVaugh, Mem. New York Bot. Gard. 10: 81. 1958. TYPE: Venezuela. Amazonas: Cerro de la Neblina, Rio Yatua. 23 Dec. 1953, *B. Maguire 36820* (holotype, MICH-1109606!; isotypes, K-00036836!, NY-00563996!, US-00036836!, VEN-41584!). [Species group B].

Habitat and distribution. *Myrcia caesariata* was collected on the Cerro de la Neblina, Amazonas Province, Venezuela, at altitudes of ca. 650–700 m.

IUCN Red List category. *Myrcia caesariata* is known only from the type specimen collected in 1953, from what is now the relatively inaccessible Médio Rio Negro II Indigenous Reserve (WDPA, 2015). Until more fieldwork in and around the type locality is undertaken, it is impossible to comment on the conservation status of the species. The species is assessed as Data Deficient (DD) according to IUCN criteria (2014).

Notes. *Myrcia caesariata* is a larger-leaved species, with blades to 21 cm, possibly related to McVaugh's (1958) *Marlierea* sect. *Myrciopsis* based on the possession of mixed terminal and lateral bunches of reduced cymose panicles. Flowers are

completely closed in the bud; panicles and buds are covered with dense, red, felty hairs.

- 15. *Myrcia calcicola*** Proctor, J. Arnold Arbor. 63: 281. 1982. TYPE: [Jamaica.] E slope of John Crow Mtns., 1.5–2.5 mi. S of Ecclesdown, 27 July 1963, G. R. Proctor 23871 (holotype, A-00071063!; isotype, GH-00071064!). [Species group B].

Habitat and distribution. *Myrcia calcicola* is a montane species endemic to Jamaica at altitudes of ca. 1500–2500 m.

IUCN Red List category. *Myrcia calcicola* is known only from the type, which we have not been able to view. *Myrcia calcicola* is assessed as Data Deficient (DD) according to IUCN criteria (2014).

Notes. The original description of *Myrcia calcicola* indicates four calyx lobes that fall cleanly from the hypanthium and a cymose, terminal inflorescence. We cautiously assign this species to *Myrcia* sect. *Aulomyrcia*. *Myrcia calcicola* was listed by Adams (1972: 517) as “species A”; however, a duplicate of the type collection was apparently not deposited in Jamaica.

- 16. *Myrcia cana*** (McVaugh) E. Lucas & C. E. Wilson, comb. nov. Basionym: *Marlierea cana* McVaugh, Mem. New York Bot. Gard. 10: 82. 1958. TYPE: Venezuela. Amazonas: Cerro Duida, Rio Cunucunuma, 22 Nov. 1950, B. Maguire 29653 (holotype, MICH-1109605!; isotypes, NY-405291!, VEN-41604!). [Species group B].

Habitat and distribution. *Myrcia cana* is known from higher altitudinal forests of Amazonas Province, Venezuela, from altitudes of 1100–1800 m.

IUCN Red List category. *Myrcia cana* has an EOO of ca. 500 km² and is known from only three collections. This species has been collected within the Duida-Marahuaca National Park (WDPA, 2015); at the time of writing, this park is not locally respected (EOE, 2015). *Myrcia cana* is assessed as Endangered (EN) according to IUCN criteria (2014).

Notes. *Myrcia cana* is an unusual species with shortly petiolate, coriaceous, revolute leaves, shiny adaxially, with a convex midvein and darkened petioles. Inflorescences are mixed axillary and terminal paniculate cymes with broad, flattened rachises. Buds are completely closed, the calyx

tearing open into extremely irregular lobes to a nearly perfect calyptra. The flowers and fruits dry black and are covered in pale hairs; fruits are globose with a neat ring of hypanthial remains similar to those in clade 7 of Lucas et al. (2011). The tearing calyx and a somewhat zigzagged arrangement of the primary axis of the inflorescence place the species in *Myrcia* sect. *Aulomyrcia*.

Selected specimen. VENEZUELA. **Amazonas:** Atabapo, Serrania del Paru (Aroko), Huber 4337 (K, NY).

- 17. *Myrcia caudata*** (McVaugh) E. Lucas & C. E. Wilson, comb. nov. Basionym: *Marlierea caudata* McVaugh, Fieldiana, Bot. 29: 176. 1956. TYPE: Peru. Loreto: Mishuyacu, near Iquitos, Oct.–Nov. 1929, G. Klug 235 (holotype, F-0040040F!; isotypes, NY-00405292!, US-00117784!). [Species group B].

Habitat and distribution. *Myrcia caudata* has been collected from forests of southern Venezuela to Peru at an altitude of ca. 100 m.

IUCN Red List category. *Myrcia caudata* is a widespread species known to us from over 30 collections from more than 20 independent localities and well represented in online herbaria (EOO > 1.6 million km²). The species is of Least Concern (LC) according to IUCN criteria (2014). Holst (2002) provided further description and suggested unqualified affinity to *M. neoschomburgkiana*.

Notes. *Myrcia caudata* is a species with short (to 5 cm), pronounced acuminate leaves with somewhat blunt acumen, no secondary venation, and a raised midvein. Inflorescences are mixed terminal and lateral bunches of panicles reduced to appear racemose in places, with flattened rachises and covered with silky hairs. The calyx appears to fall cleanly from the globose fruit, leaving a smooth, circular scar.

Selected specimens. BRAZIL. **Acre:** vic. Serra da Moa, Prance 12299 (K). **Amazonas:** Manaus, Res. Flor. Ducke, Manaus–Itacoatiara, Km. 26, Vicentini 542 (K). **Mato Grosso:** Sinop, 7 km E of BR 163 N of Rio Celeste, 51 km S of Sinop, Thomas 3864 (K). **Pará:** BR 163, Cuiabá–Santarém Hwy., Km. 1234, Prance 25536 (K). **Rondônia:** Porto Velho, Represa Samuel, end of E dike rd., Thomas 5095 (K). COLOMBIA. **Caquetá:** Parque Nac. Chiribiquete. Rio Cunare–Raudal del tubo, Fund. Biol. Puerti Rastrojo 57 (K). PERU. **Loreto:** Maynas, Iquitos, Nina rumi, Rio Nanay, Vasquez 8952 (NY).

- 18. *Myrcia chonodisca*** E. Lucas & C. E. Wilson, nom. nov. Replaced name: *Marlierea salticola* Amshoff, Bull. Torrey Bot. Club 75: 529. 1948,

non *Myrcia salticola* (Steierm.) McVaugh, Mem. New York Bot. Gard. 18. 1969. TYPE: British Guiana [Guyana]. Amatuk Portage: Potaro River Gorge, *B. Maguire* 23549 (holotype, NY-00405301!; isotypes, F-0065395FF!, GH-00069926!, K-000261027!, MO-313521!, P-01902220RB!, RB-00542135!, U-0008497!, U-0007908US!, US-00117791!, VEN-29052!). [Species group B].

Habitat and distribution. *Myrcia chonodisca* is apparently endemic to the Potaro River; it is described in the protologue as locally common on rocks in falls and restricted to riverbeds at an altitude of ca. 400 m.

IUCN Red List category. *Myrcia chonodisca* is known to us from two collections from close to the relatively well-collected but unprotected type locality, suggesting a restricted population. This area is not under any known immediate environmental threat, but should this change, threat would immediately increase. *Myrcia chonodisca* is assessed as Vulnerable (VU D2) according to IUCN criteria (2014).

Notes. The protologue of *Myrcia chonodisca* describes a closed bud and suggests absent petals; it further suggests an affinity with *M. neomontana* E. Lucas & C. E. Wilson that we do not detect. With groups of short cymes with flat rachises emerging at the terminal node and pointed buds, there is a strong resemblance between this species and those of *Calypttranthes*.

Selected specimen. GUYANA. **Potaro-Siparuni:** Kangaruma, Potaro River, Essequeibo, *Abraham* 337 (K).

19. *Myrcia clavija* Sobral, Novon 16: 520. 2006. TYPE: Brazil. Minas Gerais: Descoberto, 15 June 2001, *R. Forzza* 2193 (holotype, CES not seen; isotypes, RB-00542144!, RB-00722663!). [Species group A].

Habitat and distribution. *Myrcia clavija* has been collected from the Atlantic forests of Minas Gerais and is endemic to the Reserva Biológica da Represa do Grama, at altitudes of ca. 100–1000 m.

IUCN Red List category. *Myrcia clavija* is calculated in the protologue as being Data Deficient (DD) according to IUCN criteria (2014).

Notes. *Myrcia clavija* is a distinctive species with up to 10 straplike leaves whorled at a single node; the

midveins are raised and the species has multiple long, whorled, terminal panicles. *Myrcia clavija* is similar to *M. hexasticha*, *M. tetraphylla*, and their related species but differs from these in consistently having more than six leaves per node and aristate calyx lobes.

Selected specimen. BRAZIL. **Minas Gerais:** Descoberto, Res. Biol. Represa do Grama, *Lucas* 244 (K).

20. *Myrcia coelosepala* Kiaersk., Enum. Myrt. Bras. 81. 1893. TYPE: Brazil. Rio de Janeiro, Nova Friburgo, 15 Jan. 1882, *A. F. M. Glaziou* 13893 (lectotype, designated here, C-10012832!; isotypes, BR-0000005238644!, C-10015831!, F-0065459F!, F-0065462F!, F-0065461F!, F-0065464F!, F-0065460F!, G-00222564!, K-000342714!, K-000342715!, LE-00007141!, NY-405401!, P-00161311!, P-00161312!, R-000009023!, US-00048347!). [Species group C].

Aulomyrcia cambessedean O. Berg, Linnaea 27: 40. 1855, syn. nov. TYPE: [Brazil. Minas Gerais:], Carrascos, montis Serra Negra, s.d., *A. F. C. de Saint-Hilaire* 115 (lectotype, designated here, P-00161477!; isotype, P [2!]).

Myrcia amblyphylla Kiaersk., Enum. Myrt. Bras., 76. 1893, syn. nov. TYPE: [Brazil. Minas Gerais:], Caraça, 20 Feb. 1884, *A. F. M. Glaziou* 14831 (lectotype, designated here, C-10015821!; isotypes, LE-00007128!, P-00161487!).

Habitat and distribution. *Myrcia coelosepala* is found in Brazil from Bahia, Minas Gerais to São Paulo in cerrado, gallery, and Atlantic forest at altitudes of 900–1500 m.

IUCN Red List category. *Myrcia coelosepala* is known to us from six collections, with several reliably named specimens available online (speciesLink, 2015) giving an EOO of ca. 82,000 km², occurring in well-protected national parks in each of the states where it occurs. *Myrcia coelosepala* is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia coelosepala* is distinguished by its oblong-elliptic leaves with evident glands and veins abaxially; the species is distinguished from *M. obovata* (O. Berg) Nied. by its longer, normally discoloured leaves with evident venation and possession of two locules (vs. three in *M. obovata*). *Myrcia coelosepala* is distinguished from *M. littoralis* by glabrous buds and inflorescences (vs. a usual covering of trichomes in *M. littoralis*). *Myrcia littoralis* is restricted to coastal restinga vegetation, while *M. coelosepala* occurs in mountainous regions. Kiaerskou described *M. amblyphylla* at the same time as *M. coelosepala* and associated the former with

Aulomyrcia cambessedean; the only difference among these species is the more acute leaf tips of *M. coelosepala*. The three names are synonymized here, maintaining the more frequently used *Myrcia* name. The name *M. coelosepala* is selected instead of making a new combination based on the oldest basionym *A. cambessedean*. The resulting combination would be blocked by *M. cambessedesiana* O. Berg (Art. 60.7: McNeill et al., 2012).

Selected specimens. BRAZIL. **Bahia:** Palmeiras, Morro do Pai Inácio, *Giulietti* 773 (BHCB). **Minas Gerais:** Lima Duarte, Parque Estadual da Serra do Ibitipoca, *Lucas* 267 (K). **Rio de Janeiro:** Nova Friburgo, Morro Curusu, 15 July 1987, *Pessoa* 181 (RB); Itatiaia, 1918, *Campos Porto* 710 (RB). **São Paulo:** Capital, nativa no Jardim Botânico, *Kuhlmann* 3343 (K).

21. *Myrcia colpodes* Kiaersk., Enum. Myrt. Bras., 80. 1893. TYPE: Brazil. Rio de Janeiro: Praia Grande, au Morro da Viração, 12 Mar. 1862, *A. F. M. Glaziou* 832 (lectotype, designated here, C-10015833!; isoelectotypes, BR-0000005238972!, BR-0000005239917, C-10015834!, P-00161301!). [Species group A].

Habitat and distribution. *Myrcia colpodes* is known from littoral areas (restinga), and Atlantic rainforests of southeastern Brazil (Rio de Janeiro) at an altitude of ca. 20 m.

IUCN Red List category. *Myrcia colpodes* is known only from the type and one other 19th century collection from a relatively well-collected area; this species has an extremely restricted population. The Atlantic forests of Rio de Janeiro are under constant and immediate threat from anthropogenic developments. This species is assessed as Critically Endangered (CR) according to IUCN criteria (2014).

Notes. *Myrcia colpodes* has pubescent branchlets, long, coriaceous leaves with raised midveins, and long, whorled, terminal inflorescences to 22 cm. *Myrcia colpodes* is similar to species such as *M. eumecephylla*, *M. gigantea*, or *M. hexasticha*, but it is distinct from these in its markedly bullate leaves.

Selected specimen. BRAZIL. **Rio de Janeiro:** Cova de Onça, *Glaziou* s.n. (K).

22. *Myrcia compta* McVaugh, Mem. New York Bot. Gard. 18: 82. 1969. TYPE: Venezuela. Cerro Sipapo, 14 Jan. 1949, *B. Maguire* 28338 (holotype, MICH-1109473!; isotypes, NY-00405402!, S-052415!, US-0011774!, VEN-75724!). [Species group B].

Habitat and distribution. *Myrcia compta* is endemic to the forests of Venezuela, Amazonas Province, from altitudes of ca. 1600–2000 m.

IUCN Red List category. *Myrcia compta* is known only from the type and paratype collections, all from the Cerro Sipapo, a relatively poorly known and collected area. This species appears to have an extremely restricted EOO. The forests of the Cerro Sipapo are, however, protected by the Sipapo Forest Reserve. The species is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia compta* is a species with coriaceous, sharply acuminate, discolourous, leaves with revolute margins and raised midribs on both faces of the blades. Aggregations of short, lateral, reduced inflorescences covered in silky red hairs suggest a relationship with species of McVaugh's (1958) *Marlierea* sect. *Myrciopsis*.

23. *Myrcia connata* McVaugh, Fieldiana, Bot. 29: 189. 1956. TYPE: Bolivia. La Paz: S Yungas, basin of Rio Bopi, San Bartolome (near Calisaya), 1–22 July 1939, *B. A. Krukoff* 10382 (holotype, NY-00004779!; isotypes, A-00071082!, CAS-0003587!, F-0065463F!, LP-010394!, MICH-1109470!, MO-313565!, S-052418!, U-0005100!, US-00117742!, WIS-00000205!). [No species group assignment].

Habitat and distribution. *Myrcia connata* is known from Bolivian “bosque primario” at altitudes of 750–900 m.

IUCN Red List category. *Myrcia connata* is known to us only from the type; we could find no additional information regarding environmental threat to the type locality. *Myrcia connata* is assessed as Data Deficient (DD) according to IUCN criteria (2014).

Notes. *Myrcia connata* is distinct in having cordate, connate leaf bases and hispid branchlets. Inflorescences are terminal or subterminal. Leaves are decussate; the midvein is concave. The hypanthium, petals, and calyx lobes bear silky golden hairs. The hypanthium is somewhat ridged, calyx lobes are broad and blunt, and the disk is hairy. Despite sharing characters of silky pubescence with species previously accepted in *Gomidesia*, we ascribe the species to *Myrcia* sect. *Aulomyrcia* based on the leaf and inflorescence architecture and extended hypanthium.

24. *Myrcia convexivenia* (B. Holst) E. Lucas & C. E. Wilson, comb. nov. Basionym: *Marlierea convexivenia* B. Holst, Selbyana 23: 144. 2002. TYPE: Venezuela. Amazonas: Casiquiare, Caño San Miguel, sector Las Tinajas y el Caño Iqueven, 24 Apr. 1991, G. Aymard 9151 (holotype, PORT-58161!; isotype, SEL-003102!). [Species group B].

Habitat and distribution. *Myrcia convexivenia* has been collected from white sand and scrub forests along black water rivers in southern Venezuela at an altitude of ca. 200 m.

IUCN Red List category. *Myrcia convexivenia* is known from the four collections cited in the protologue that give an EOO of ca. 20,000 km², the limit for an IUCN (2014) category of threat. The species is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia convexivenia* is contrasted in the protologue (Holst, 2002) with *M. caesariata*. *Myrcia convexivenia* differs in having narrower leaves and unusually racemose inflorescences; this is evident from the type collection.

Selected specimen. VENEZUELA. **Amazonas:** “Sabana Grande” del Río Pasimoni, a altura de Pueblo Viejo, Stergios 13341 (NY).

25. *Myrcia decorticans* DC., Prodr. [de Candolle] 3: 252. 1828. *Aulomyrcia polymorpha* O. Berg var. *decorticans* (DC.) O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14: 78. 1857. TYPE: [Brazil.] Brasilia, s.d., C. F. P. Martius s.n. (lectotype, designated here, M-0136901!; isotype, M-0136900!). [Species group C].

Aulomyrcia salzmannii O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14: 116. 1857, syn. nov. TYPE: [Brazil. Bahia], s.d., P. Salzmann 279 (lectotype, designated here, G-00222034!; isotype, G-00222035!).

Habitat and distribution. *Myrcia decorticans* is a forest species distributed from Tobago to northeastern Brazil at altitudes from 100 to 700 m.

IUCN Red List category. *Myrcia decorticans* is a widespread species known to us from 50 collections from 30 localities and is well represented in online herbaria. It has an EOO > 1.6 million km²; the species is of Least Concern (LC) according to IUCN criteria (2014).

Notes. McVaugh (1969) followed Berg (1855–1856) in accepting multiple species in synonymy of *Myrcia decorticans* (in the case of Berg, under *Aulomyrcia polymorpha* O. Berg). It is clear from McVaugh’s discussion as well as material examined that there are distinct entities within what is currently known as *M. decorticans*. Most obviously, the type specimen from Bahia is a stouter, more pubescent species than any collection made from the Amazon, the Guianas, or the Antilles; there are also differences in inflorescence architecture. The entities are united in having internally pubescent calyx lobes, somewhat open venation, and apiculate leaves. Amazonian collections can have corky petioles and the largest (up to 2 cm diameter) fruits in the *decorticans* complex of Holst (2002). These entities are here treated together; however, it is clear that more detailed study is required.

Selected specimens. BRAZIL. **Bahia:** Mata de São João, Praia do Forte, na beira da avenida de entrada, Lima 406 (K). **Sergipe:** Crasto, ca. 2 km na estrada Crasto para Santa Luzia do Itanhi, de Carvalho 4345 (NY). FRENCH GUIANA. Crique Kulumuli, Mont Saint-Marcel, Bassin de l’Oyapock, Sastre 4634 (CAY). GUYANA. **Pomeroon-Supenaam:** Chaakoitou, near Mtn. Point, S of Kanuku Mtns. forest near Tutuwau Falls, Maas 4053 (K). VENEZUELA. **Bolívar:** NE of Upata, El Paráiso camp, Breteker 5088 (K).

26. *Myrcia diaphana* (O. Berg) N. Silveira, Roessleria 7: 66. 1985. Basionym: *Aulomyrcia diaphana* O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14: 82. 1857. TYPE: [Brazil.] São Paulo, s.d., F. Sellow s.n. (holotype, B†; lectotype, designated here, K-000342814!; isotype, BR-0000005280582!, F-0064708F!, LE-00007051!, P-00163051!, P-00163052!). [Species group C].

Habitat and distribution. *Myrcia diaphana* was collected from forested hills of southeastern Brazil from an altitude not precisely known.

IUCN Red List category. *Myrcia diaphana* is known only from the type from an unspecified locality. It is assessed as Data Deficient (DD) according to IUCN criteria (2014).

Notes. *Myrcia diaphana* is a bilocular species strongly resembling *M. multiflora* in leaf shape, texture, and venation. It is known only from the type; it is possible that this is synonymous with that latter species.

27. *Myrcia dichrophylla* D. Legrand, Sellowia 13: 294. 1961. TYPE: Brazil. Santa Catarina: Monte

Crista, Garuva, S. Francisco do Sul, 22 Dec. 1957, *R. Reitz* 5908 (holotype, MVM not seen; isotypes, HAS not seen, HBR not seen, HUEFS not seen, MBM not seen, NY not seen, PACA not seen, US-00117747!). [Species group C].

Habitat and distribution. *Myrcia dichrophylla* is found from Rio de Janeiro to Rio Grande do Sul from coastal restinga and dense ombrophilous forests at altitudes of 0–500 m.

IUCN Red List category. *Myrcia dichrophylla* is known to us from seven collections but reliably named collections are common in online specimen databases (speciesLink, 2015), giving an EOO of ca. 80,000 km². *Myrcia dichrophylla* is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia dichrophylla* is recognized by its discolored and completely glabrous leaves.

Selected specimens. BRAZIL. **Paraná:** Guaratuba, Brejatuba, *Silva* 1015 (MBM). **Santa Catarina:** Florianópolis, Morro do Ribeirão, *Klein* 7394 (MBM). **São Paulo:** Iguape, Estação Ecológica Juréia-Itatins, *Nicolau* 254 (SP).

28. *Myrcia egensis* (O. Berg) McVaugh, Fieldiana, Bot. 29: 191. 1956. Basionym: *Aulomyrcia egensis* O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14: 99. 1857. TYPE: [Brazil.] Amazonas: Solimões, 1831, *E. F. Poeppig* 2551 (lectotype, designated here, W-0033253!; isoelectotypes, F-0064711FF!, G-00222531G!, W-0032623!, W-18890212639!). [Species group C].

Habitat and distribution. *Myrcia egensis* is noted from moist forests in northern Brazil to Peru; its altitude is not precisely known.

IUCN Red List category. *Myrcia egensis* is known to us only from the type from an unspecified locality in Brazil. Material from Peru was cited by McVaugh (1963) that increased the EOO of this species and suggested an unconfirmed altitude of 1200–1300 m. More information on those collections and threats to these areas is required before a category of threat is assigned. For now, the species is Data Deficient (DD) according to IUCN criteria (2014).

Notes. *Myrcia egensis* is a distinctive species with discolored leaves and open venation. The inflorescences are in terminal axils, in short, distinctive, asymmetrical panicles; the fruits are covered by pale hairs and bear five calyx lobes.

Selected specimen. PERU. **San Martín:** Moyobamba, *Klug* 3569 (MO not seen).

29. *Myrcia ehrenbergiana* (O. Berg) McVaugh, Mem. New York Bot. Gard. 18: 85. 1969. Basionym: *Myrciaria ehrenbergiana* O. Berg, Linnaea 27: 321. 1856. *Aulomyrcia ehrenbergiana* (O. Berg) Amshoff, Recueil Trav. Bot. Néerl. 42: 8. 1950. TYPE: British Guiana. Roraima, 1842–1843, *Rob. Schomburgk* 700 (lectotype, designated here, W-0029521!; isoelectotypes, BM-000953656!, G-00222404!, K-000342848!, K-000342849!, MICH-1109534!, P-00735122!, P-00735123!, U-0046438!, W-18890013678!). [No species group assignment].

Habitat and distribution. *Myrcia ehrenbergiana* is a montane species distributed from northern South America to northern Brazil from an altitude of ca. 1065 m.

IUCN Red List category. *Myrcia ehrenbergiana* is known to us from eight collections from seven independent localities, giving an EOO of ca. 34,000 km². This EOO falls beyond the IUCN criteria of threat; however, the relatively few and far apart locations from which the specimens have been located suggest a fragmented population. Therefore, *M. ehrenbergiana* is assessed as Near Threatened (NT) according to IUCN criteria (2014).

Notes. *Myrcia ehrenbergiana* is a distinctive species with subsessile, cordate, lustrous leaves with revolute margins and 4-merous flowers. This species has a flat to raised midvein adaxially and a concentration of long, asymmetrical inflorescences toward the ends of the branchlets. *Myrcia ehrenbergiana* is reminiscent of *M. subulata* in having a terminal inflorescence; however, the inflorescence is not whorled or subtended by foliaceous bracts.

Selected specimens. BRAZIL. **Roraima:** Vitoria, Serrinha, Rio Mucajai, summit of serra, *Prance* 4225 (K). GUYANA. **Upper Takutu–Upper Essequibo:** S Pakaraima Mtns., Tipuru River, 4 km upstream from Ireng River, trail to Tipuru village, *Hoffman* 1908 (K); Kanuku Mtns., *Jansen-Jacobs* 278 (K).

30. *Myrcia ensiformis* (McVaugh) E. Lucas & C. E. Wilson, comb. nov. Basionym: *Marlierea ensiformis* McVaugh, Mem. New York Bot. Gard. 18: 64. 1969. TYPE: Venezuela. Amazonas: Serra de Neblina expedition, Camp 5, 24–25 Nov. 1965, *B. Maguire* 60418 (holotype, MICH not seen; isotypes, MIN-1002847!, MO-313523!,

NY-563997!, US-00117786!, VEN-411284!). [Species group B].

Habitat and distribution. *Myrcia ensiformis* was collected from the Serra da Neblina, on the borders of southern Venezuela and northern Brazil; the species is recorded from an altitude of ca. 750 m.

IUCN Red List category. *Myrcia ensiformis* is known only from the type collection. The area in which it was collected is unprotected (WDPA, 2015); however, due to the inaccessibility of the area, the ecoregion is largely intact (EOE, 2015) and the species remains poorly collected. Until more field-work is undertaken in this area, it is difficult to determine if the distribution of this species has been reduced or whether the species is simply rare. This is assessed as Data Deficient (DD) according to IUCN criteria (2014).

Notes. McVaugh (1969) was unsure of the affinities of *Myrcia ensiformis*, but, based on its winged internodes, terminal and axillary cymose inflorescences with flattened axes, and prolonged hypanthia splitting between the calyx lobes, he associated his *Marlierea ensiformis* with *Marlierea* sect. *Myrciopsis*. In leaf and inflorescence architecture, this species is similar to *Myrcia caesariata* and *M. biptera*; however, in *M. ensiformis*, although the calyx lobes are irregular, there was no tendency observed for one larger lobe to appear calyptrate. Leaves reach 16 cm; the whole plant is glabrous.

31. *Myrcia eumecephylla* (O. Berg) Nied., Nat. Pflanzenfam. 3(7): 76. 1893. Basionym: *Aulomyrcia eumecephylla* O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14: 98. 1857. TYPE: [Brazil.] São Paulo, s.d., *F. Sellow* s.n. (holotype, B†; lectotype, designated here, LE-00007060!). [Species group A].

Myrcia limae G. M. Barroso & Peixoto, Acta Bot. Brasil. 4 (2): 11. 1990, syn. nov. TYPE: [Brazil.] Espírito Santo: Reserva Biol. Sooretama, Aug. 1969, *D. Sucre* 9660 (lectotype, designated here, RB-00542154!; isoelectotype, RB-00557164!).

Habitat and distribution. *Myrcia eumecephylla* is known from tabuleiro and ombrophilous Atlantic forest of Brazil (southern Bahia and Espírito Santo to São Paulo); it is noted from altitudes of ca. 5–200 m.

IUCN Red List category. The type of *Myrcia eumecephylla* was from São Paulo; it has not been recollected at the type locality since the mid-19th century. Collections available online (speciesLink,

2015) indicate further collections from southern Bahia and the EOO is greater than that required to assign an IUCN category of threat. However, the species has only recently been collected from Espírito Santo from sites within 100 km of each other, and threats to this part of the Atlantic forest are high. The species grows within the Sooretama Biological Reserve, and, with this protection in place, the species should be secure. It is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia eumecephylla* is a species distinguished by its large (to 30 cm), subsessile leaves; cordate bases and raised adaxial midveins on blades; and terminal, decussate inflorescences to 20 cm with persistent, foliaceous bracts and sessile flowers. This species has an affinity with species such as *M. gigantea*, *M. hexasticha*, *M. neoverticillaris* E. Lucas & C. E. Wilson, and *M. insularis*.

Selected specimen. BRAZIL. **Espírito Santo:** Reserva Nat. Vale, 11 Sep. 2009, *Folli* 6414 (K).

32. *Myrcia excoriata* (Mart.) E. Lucas & C. E. Wilson, comb. nov. Basionym: *Marlierea excoriata* Mart., Flora 20 (2 Beibl.): 88. 1837. TYPE: [Brazil.] Corcovado et alibi in nemoribus prov. Rio de Janeiro, 1837, *C. F. P. Martius* 59 (lectotype, designated here, BR-0000005299362!; isoelectotypes, E-00433027!, G-00223337!, K-000330690!, M-0171101!, MO-176997!, NY-00405294!, P-00217945!, P-00217946!). [No species group assignment].

Marlierea parviflora O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14: 537. 1859. TYPE: [Brazil.] In silvis umbrosis montosis montium Serra d'Estrella, Feb. 1824, *L. Riedel* s.n. (lectotype, designated here, LE-00004034!; isoelectotypes, G-00223345!, K-000330492!, K-000330693!, LE [2]!, M!, MO-2386046!, NY-405300!, S-052560!, U-0005080!).

Habitat and distribution. *Myrcia excoriata* is known from the Atlantic forests of eastern and southern Brazil (Bahia to Rio Grande do Sul) from 50 to 1500 m.

IUCN Red List category. *Myrcia excoriata* is known to us from 21 collections from 18 localities with an EOO > 650,000 km². *Myrcia excoriata* is considered of Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia excoriata* has short, terminal, and axillary inflorescences to 6(–7) cm, with small persistent triangular bracts below the flowers. Flowers tear into the staminal disk giving a characteristic 5-pointed star appearance. Bark peels in thin strips

from branchlets. Specimens collected south of São Paulo are consistently somewhat different from the type, with slightly thicker, discolored leaves and wider, flattened inflorescence rachises. Legrand and Klein (1971) described this material as *Marlierea parviflora*, now synonymous with *Myrcia excoriata* (Sobral et al., 2015). *Myrcia excoriata* is similar to *M. obscura* (O. Berg) N. Silveira but differs in having smaller, more acuminate leaves.

Selected specimens. BRAZIL. **Bahia:** Valença, Estrada Valença/Guaibim, Km. 10, *de Carvalho 1128* (K). **Espírito Santo:** 1 km W of Venda Nova de Imigrante, 5–7 km de la rod. BR 262, *Arbo 7746* (K). **Minas Gerais:** Reserva Biol. da Represa do Gramma, trilha principal partindo da casa de Seu Luiz, *Lucas 233* (K). **Paraná:** Bocaiúva do Sul, Trilha na borda do Rio Capivari, *Lucas 151* (K). **Rio de Janeiro:** Guanabara, Morro Taquara da Tijuca, *Sucre 8180* (K). **Santa Catarina:** Matador, Rio do Sul, *Reitz 7336* (K).

33. *Myrcia exploratoris* McVaugh, Mem. New York Bot. Gard. 18: 86. 1969. TYPE: Venezuela. Bolívar: upper slopes of Carrao-tepuí, 7 Dec. 1944, *J. A. Steyermark 60879* (holotype, F-0065481F!; isotype, U-0005140!). [Species group C].

Habitat and distribution. *Myrcia exploratoris* is found in Guyana, Suriname, and Venezuela at altitudes above 2000 m.

IUCN Red List category. *Myrcia exploratoris* is known to us from three collections from two localities. These in addition to three reliably named collections available online (TROPICOS®, 2015) give an EOO of ca. 45,000 km², disqualifying it from a category of threat (IUCN, 2014). However, the species is known from high elevations only and as such will have a considerably smaller real distribution. The Myrtaceae of the Guiana Highlands are relatively well known (McVaugh, 1958, 1969), suggesting that the low number of collections reflects a rare species. However, no specific threat is known to any of the regions from which the species has been found; it was last collected in 1991. It is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia exploratoris* has obovate leaves held erect on the branch; in this respect, and in respect of the silky hairs that cover the inflorescence and hypanthium, it resembles *M. littoralis*. The distribution is widely disjunct, however, and the latter species occurs exclusively close to sea level. The leaves of *M. exploratoris* are larger and more coriaceous than those of *M. littoralis*. The leaves and general architecture of *M. exploratoris* are reminis-

cent of *M. platyclada* as the latter species is also glabrous.

Selected specimens. GUYANA. **Cuyuni-Mazaruni:** Paruima, 15 km W, 0.25 km E of camp near eastern summit of Waukauyengtipu, *Clarke 5735* (K). VENEZUELA. **Bolívar:** Meseta del Jaua, Cerro Jaua, *Steyermark 109545* (K).

34. *Myrcia extranea* McVaugh, Mem. New York Bot. Gard. 18: 87. 1969. TYPE: British Guiana. Kaiteur Plateau, near Kaiteur Falls, 20 Mar. 1962, *R. S. Cowan 2248* (holotype, MICH-1109521!; isotypes, K-000342850!, NY-00004781!, US-00117750!). [No species group assignment].

Habitat and distribution. *Myrcia extranea* was collected from the Kaiteur Plateau near Kaiteur waterfall in Guyana at an altitude of ca. 400 m.

IUCN Red List category. *Myrcia extranea* is known to us only from the type and paratype specimens from a single locality, suggesting a restricted population from a relatively well-collected area. Protection offered by the Kaiteur National Park prevents an environmental threat category for this species, which is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. The protologue for *Myrcia extranea* suggested an affinity with *M. minutiflora*, although McVaugh (1969) commented on the need for flowering material. The type specimen has leaves with rather open venation and shortened pedicels very similar to *M. minutiflora* but differs in having persistent calyx lobes and pubescence on the interior of the hypanthium (McVaugh, 1969).

35. *Myrcia ferruginea* (Poir.) DC., Prodr. [de Candolle] 3: 245. 1828. Basionym: *Eugenia ferruginea* Poir. in J. B. A. P. M. de Lamarck, Encycl., Suppl. 3: 124. 1813. *Marlierea ferruginea* (Poir.) McVaugh, Mem. New York Bot. Gard. 10: 83. 1958. *Krugia ferruginea* (Poir.) Urb., Bot. Jahrb. Syst. 19(5): 604. 1895. *Myrtus ferruginea* (Poir.) Spreng., Syst. Veg. 2: 487. 1825. TYPE: [French Guiana.] Cayenne, s.d., *herb. Poiret s.n.* (lectotype, designated here [likely holotype], P-01817729!). [Species group B].

Habitat and distribution. *Myrcia ferruginea* occurs on the Windward Islands and in northwestern South America between altitudes of 250 and 1700 m.

IUCN Red List category. *Myrcia ferruginea* is a widespread species with an EOO > 300,000 km².

The species is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. *Krugia* was distinguished from *Myrcia* by Urban (1893) based on the petals that adhere to the calyx. *Myrcia ferruginea* is very distinctive with dense, ferruginous indumentum and a terminal inflorescence with bracts at the nodes. The overall architecture, especially of the asymmetrical inflorescence, suggests this species belongs to *Myrcia* sect. *Aulomyrcia*; Rosário and Secco (2006) suggested an affinity with *M. neovelutina* E. Lucas & C. E. Wilson. However, the poorly defined calyx lobes and partial hypanthial tearing are also reminiscent of species previously described in *Eugeniopsis* O. Berg (Santos, pers. comm.).

Selected specimens. COLOMBIA. **Caquetá:** Parque Nacional Chiribiquete, Rio Mesay, Jacamiya Raudal, *Fundacion Biologica Puerti Rastrojo CHI22* (K). FRENCH GUIANA. Grand Inini, Saut Batadeau, *de Granville B3788* (K). GRENADA. Grand Etang, *Beard 590* (K). GUYANA. **Cuyuni-Mazaruni:** N foothills of Roraima, betw. camps 3 & 4, *Hahn 5357* (CAY). ST. VINCENT. s. loc., s.d., *Smith s.n.* (K). SURINAME. **Marowijne:** Lely Mtns., airstrip, plateau, lateritic rocky soil, *Jansen-Jacobs 6720* (K). TRINIDAD AND TOBAGO. Aripo Rd., 5 mi. post, *Broadway 6556* (K). VENEZUELA. **Bolívar:** Piar, Rio Aparaman, affluent of Rio Acanan, *Holst 3475* (K).

36. *Myrcia fusca* B. Holst & M. L. Kawas., Selbyana 25: 95. 2004. TYPE: Panama. El Llano–Cartí Rd., 9.6–11 km from Inter-American Hwy., 4 Dec. 1974, *S. Mori 3541* (holotype, MO-671228!; isotypes, MICH not seen, PMA not seen, SEL not seen). [Species group C].

Habitat and distribution. *Myrcia fusca* is found in the wet forests of Panama at altitudes of ca. 30–500 m.

IUCN Red List category. *Myrcia fusca* is known to us from the type and four authoritatively identified specimens from TROPICOS® (2015) that give an EOO of ca. 30 km². The species has been relatively well collected and recently collected; the restricted distribution in unprotected forest, however, makes it vulnerable to stochastic change and is assessed as Vulnerable (VU D2) according to IUCN criteria (2014).

Notes. The protologue links *Myrcia fusca* with the decorticans complex of Kawasaki and Holst (1994) and reports *M. fusca* to be the northernmost species in the complex. The species is distinguished by sessile, cordate leaves with impressed secondary venation. The inflorescence is terminal with long axes (to 15 cm) with architecture similar to that of the

littoral Atlantic forests such as *M. hexasticha*; however, the inflorescence of *M. fusca* is not whorled. *Myrcia fusca* recalls *M. subulata*.

37. *Myrcia gentryi* B. Holst, BioLlania 10: 4. 1994. TYPE: Venezuela. Amazonas: Atabapo, Cerro Huachamacari, 1 Mar. 1985, *R. Liesner 18140* (holotype, MO-313563!; isotypes, NY-1051785!, SEL-001749!, VEN-365080!). [Species group B].

Habitat and distribution. *Myrcia gentryi* is found in gallery forest and open areas of Venezuela at an altitude of ca. 1700 m.

IUCN Red List category. *Myrcia gentryi* is known only from the type collection from a relatively poorly known and collected area. This species appears to have a restricted EOO. Nevertheless, Cerro Huachamacari is protected in the Duida-Marahuaca National Park. *Myrcia gentryi* is of Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia gentryi* is remarkable in its small leaves (to 2 cm) and its uniflorous 4- or 5-merous inflorescences, extremely rare in *Myrcia*. The protologue compares this species to *M. minutiflora*, *M. bolivarensis*, and *M. uniflora* (McVaugh) E. Lucas & C. E. Wilson.

38. *Myrcia gigantea* (O. Berg) Nied., Nat. Pflanzenfam. 3(7): 76. 1893. Basionym: *Aulomyrcia gigantea* O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14: 548. 1859. TYPE: [Brazil. Bahia:] Ilheos [Ilheus], 1859, *L. Riedel s.n.* (lectotype, designated here, LE-00007069!; isoelectotypes, F-0064729F!, K-000343087!, LE-00007065!, LE-00007066!, LE-00007067!, LE-00007068!, LE-00007070!, P-00163071!, P-00163072!). [Species group A].

Habitat and distribution. *Myrcia gigantea* is found in the Atlantic rainforest of Brazil (Bahia, also reported from Rio de Janeiro) at altitudes of ca. 0–70 m.

IUCN Red List category. *Myrcia gigantea* is known to us only from the type; specimens authoritatively identified from the NYBG virtual herbarium (Thiers, 2015) produce an EOO of ca. 200 km² from a biome that is under intense environmental threat. *Myrcia gigantea* is assessed as Endangered (EN) according to IUCN criteria (2014).

Notes. *Myrcia gigantea* has particularly large, subsessile leaves (to 30 cm) with cordate bases and a raised midvein. The inflorescence is terminal with a short, red pubescence and is whorled and subtended by large foliaceous bracts. This species has an affinity with species such as *M. eumecephylla*, *M. hexasticha*, *M. neoverticillaris*, and *M. insularis*. Sobral et al. (2015) also reported this species from the state of Rio de Janeiro.

39. *Myrcia gilsoniana* G. M. Barroso & Peixoto, Acta Bot. Brasil. 4(2): 7. 1990. TYPE: [Brazil.] Espírito Santo: Linhares, Reserva Florestal da CVRD, Rio Barra Seca, 8 Nov. 1972, J. Spada 57 (holotype, RB-00542147!). [No species group assignment].

Habitat and distribution. *Myrcia gilsoniana* is endemic to the Reserva Vale do Rio Doce, Brazil (Espírito Santo), and is found at altitudes of ca. 10–30 m.

IUCN Red List category. *Myrcia gilsoniana* is known to us only from the type specimen, suggesting an extremely restricted population from a well-collected area in a biome under extreme environmental threat. *Myrcia gilsoniana* is assessed as Critically Endangered (CR) according to IUCN criteria (2014).

Notes. The protologue of *Myrcia gilsoniana* suggests an unqualified affinity with *M. stictophylla* (O. Berg) N. Silveira, a morphologically very similar species. About six collections available online (speciesLink, 2015) indicate a species with somewhat thickened leaves and a thick midvein that decreases steadily in width toward the leaf tip.

40. *Myrcia graciliflora* Sagot, Ann. Sci. Nat., Bot., VI, 20: 185. 1885. *Eugenia schaueriana* Miq., Linnaea 22: 174. 1849. *Myrciaria schaueriana* (Miq.) O. Berg, Linnaea 27: 323. 1856. *Aulomyrcia schaueriana* (Miq.) Amshoff, Recueil Trav. Bot. Néerl. 39: 155. 1942. TYPE: Suriname. Pará, Feb.–Apr. 1844, A. Kappler 1429 (holotype, U-0005115!; isotypes, C-10015846P!, P-00549012!, S-079893!). [No species group assignment].

Habitat and distribution. *Myrcia graciliflora* occurs in the forests of northern South America, from French Guiana, Guyana, Suriname, and Brazil and has been collected at altitudes from 20 to 300 m.

IUCN Red List category. *Myrcia graciliflora* is a widespread species known to us from 24 collections from 19 localities and is very well represented in online herbaria (EOO > 2 million km²). *Myrcia graciliflora* is of Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia graciliflora* is distinguished by its relatively large, acuminate leaves (to 15 cm), often with evident glands. The inflorescence is a lateral or terminal, cymose panicle, or a mixture of the two, with a peduncle so short the impression can be of fasciculate racemes. The branches of the inflorescence can vary in length but are usually slender. The calyx is completely fused in the bud but once split into four calyx lobes, the splits do not extend into the staminal ring. McVaugh (1969) reported this to be a little known species; since that work, it is now also known from Brazil. The affinities of this species are unknown.

Selected specimens. BRAZIL. Acre: Rio Branco, Estrada Rio Branco/Quixada, Km. 11, Nelson 733 (K). Roraima: Vitoria, Serrinha, Rio Mucajai, Prance 4188 (K). FRENCH GUIANA. Crique Calebasse, Bassin de l'Approuague, Oldeman 101 (K). GUYANA. Barima River, 12 mi. E of Arakaka, at Tenap, Barima-Waini, Pipoly 8107 (K). SURINAME. Pará, Mapane, Bosbeheer 9835 (K).

41. *Myrcia grandis* McVaugh, Mem. New York Bot. Gard. 18: 114. 1969. TYPE: Venezuela. Amazonas: Rio Siapa, Casiquiare, 9 Feb. 1954, B. Maguire 37617 (holotype, MICH-1109512!; isotypes, NY-00405440!, VEN-76131!). [Species group C].

Habitat and distribution. *Myrcia grandis* is known from Igapó forest along rivers and in flooded areas from Panama to northern Brazil at altitudes of ca. 100–130 m.

IUCN Red List category. *Myrcia grandis* is a widespread species known to us from 16 collections from 16 localities and is very well represented in online herbaria (EOO > 800,000 km²). The species is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia grandis* has distinctive coriaceous leaves, which are rounded at the base and apiculate with a raised midvein. Authoritatively identified specimens cited on TROPICOS® (2015) voucher the occurrence of this species in Colombia and Panama. McVaugh (1969) commented on the 4-merous flowers, anomalous in *Myrcia*, and large free

calyx lobes permanently united at the base that excluded it from *Marlierea*.

Selected specimens. BRAZIL. **Amazonas:** along Cuiuni Rivers (blackwater), *Acevedo-Rodríguez* 8521 (K). **Pará:** Oriximina, Area de Mineracao, Rio Norte, Lago da Batata, 9 km da vila residencial, *Cid Ferreira* 9593 (K). **Roraima:** Caracarai, rd. Manaus–Caracarai, Km. 592 a 609, *dos Santos* 735 (K). GUYANA. Upper Takutu–Upper Essequibo, Kassikaityu River, 0–4 km W of landing at terminus of trail from Kuyuwini River, *Clarke* 4768 (K). VENEZUELA. **Amazonas:** Atabapo, Cabecera del Cano Cotua, Cerro Yapacans, *Huber* 1530 (K).

42. *Myrcia guildingiana* (Griseb.) E. Lucas & C. E. Wilson, comb. nov. Basionym: *Psidium guildingianum* Griseb., Fl. Brit. W. I., 242. 1860. *Marlierea guildingiana* (Griseb.) Krug & Urb., Bot. Jahrb. Syst. 19: 591. 1895. *Plinia guildingiana* (Griseb.) Urb., Ark. Bot. 21A(5): 23. 1927. TYPE: St. Vincent. Wallilabo valley, s.d., *H. H. Guilding s.n.* (lectotype, designated here, K-000330423!; isoelectotypes, GOET-007308!, K-000330424!). [Species group B].

Habitat and distribution. *Myrcia guildingiana* is reported from Venezuela, the Lesser Antilles, Guyana, and French Guiana at altitudes of ca. 120–320 m.

IUCN Red List category. *Myrcia guildingiana* is a widespread species known to us from 14 collections from 14 localities and is well represented in online herbaria (EOO > 170,000 km²). *Myrcia guildingiana* is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia guildingiana* has short, lateral inflorescences consistent with McVaugh's (1958) assignment to his *Marlierea* sect. *Myrciopsis*. Stafleu and Cowan (1976–1988) reported Guilding's top set of specimens to be deposited at GOET; however, the GOET collection consists of loose leaves and flowers only; on this basis we lectotypify the most representative sheet, housed at Kew.

Selected specimens. FRENCH GUIANA. Meamu Creek, *Redden* 4993 (K). GRENADA. Grand Etang, *Proctor* 17030 (IJ). GUYANA. **Cuyuni-Mazaruni:** Bird Island, R. B. Essequibo, opposite Bartica, *Forest Department of British Guiana* 2593 (K). ST. LUCIA. Castries, Castries Water Works Reserve, Piton Flore, *Beard* 479 (K). ST. VINCENT. Forest N side of Mt. St. Andrew, *Smith* 1735 (K). TRINIDAD AND TOBAGO. **Ward of Tobago:** Roxborough, Parlaturier Rd., *Sandwith* 1769 (K).

43. *Myrcia hexasticha* Kiaersk., Enum. Myrt. Bras., 72. 1893. TYPE: [Brazil.] Rio de Janeiro, Jan. 1881, *A. F. M. Glaziou* 11975 (holotype, C-

10015856!; isotypes, G-00439824!, K-000343357!, LE-00007167!, P-00161247!, R-000009042!). [Species group A].

Habitat and distribution. *Myrcia hexasticha* is found in the Atlantic forests of southeastern Brazil (Rio de Janeiro to Paraná) at altitudes of ca. 0–200 m.

IUCN Red List category. *Myrcia hexasticha* has been assessed as Endangered (EN) by Martinelli and Moraes (2013) according to IUCN criteria (2014).

Notes. *Myrcia hexasticha* is defined by its ternate leaf arrangement; it has raised midveins and whorled, terminal inflorescences subtended by small, leafy bracts. The species has free calyx lobes but otherwise resembles *M. neoverticillaris*; it also resembles *M. insularis*, which differs in having decussate leaves.

Selected specimens. BRAZIL. **Paraná:** Pontal do Paraná, Shangri La, *Lucas* 194 (K). **Rio de Janeiro:** Silva Jardim, *Pessoa* 1217 (K).

44. *Myrcia holstii* E. Lucas & C. E. Wilson, nom. nov. Replaced name: *Marlierea subcordata* B. Holst, Selbyana 23: 150. 2002, non *Myrcia subcordata* DC., Prodr. [de Candolle] 3: 253. 1828. TYPE: Venezuela Amazonas: Rio Baria, entre la boca de al Laguna Turuvi y la Laguna Laja Gajaio, *B. Stergios* 16348 (holotype, PORT-61500!; isotypes, MO not seen, US-00822717!, VEN-286066!). [No species group assignment].

Habitat and distribution. *Myrcia holstii* is known to us only from the type and paratype from low forests along periodically flooded riverbanks in Amazonas State, Venezuela, at an altitude of ca. 80 m.

IUCN Red List category. *Myrcia holstii* is known from only the type locality and one other locale, cited in the protologue. The locations are ca. 270 km apart, hence a very restricted EOO. The collection points do not occur in protected areas and so are vulnerable to sudden or stochastic change. *Myrcia holstii* is assessed as Vulnerable (VU D2) according to IUCN criteria (2014).

Notes. Holst (2002) associates *Myrcia holstii* with *M. argentigemma* and *M. mcvaughii* but does not qualify this. *Myrcia holstii* is unique in its subcordate leaf bases, plane abaxial midveins, and lustrous, dry leaf texture. This epithet acknowledges the significant impact of the works of Bruce K. Holst on current Myrtaceae systematics.

45. *Myrcia inaequiloba* (DC.) Lemée in Fl. Guyane Franç. 3: 150. 1954. Basionym: *Eugenia inaequiloba* DC., Prodr. [de Candolle] 3: 282. 1828. *Aulomyrcia inaequiloba* (DC.) Amshoff, Recueil Trav. Bot. Néerl. 42: 7. 1950. TYPE: French Guiana. Cayenne: s.d., collector unknown, s.n. (lectotype, designated by McVaugh [1969: 97], G-00222421!; isoelectotypes, G-DC!, L not seen). [Species group C].

Myrcia lucida McVaugh, Mem. New York Bot. Gard. 18: 100. 1969, syn. nov. *Myrcia laevis* O. Berg, Linnaea 31: 252. 1862, nom. illeg. TYPE: Venezuela. Amazonas: Rio Guainia above the mouth of the Casiquiari, 1854, R. Spruce 3502 (holotype, BR-0000005280339!; isotypes, BM-000953607!, C-10015864!, CAS-0003583!, E-00394780!, F-0065509F!, G-00222238!, K-000330179!, K-000343745!, LE-00007185!, MICH-1109507!, NY-00405447!, P-00161223!, W-18890013687!).

Myrcia lucida var. *attenuata* McVaugh, Mem. New York Bot. Gard. 18: 100. 1969, syn. nov. TYPE: Brazil. Amazonas: Porto Curucuhy, Rio Negro, 1945, R. de Lemos Fróes 21103 (holotype, MICH-1109503!; isotypes, K-000343746!, NY-00405448!).

Habitat and distribution. *Myrcia inaequiloba* is common from scrubby riversides or igapó, and from sandy soils; this species has been collected in the Amazonian forests from Panama to northern Brazil at altitudes of ca. 0–900 m. A single authoritatively named specimen of *M. lucida* collected in Bolivia (TROPICOS®, 2015) marks the species occurrence there.

IUCN Red List category. *Myrcia inaequiloba* is an extremely widespread species and is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia inaequiloba* is an extremely variable species (McVaugh, 1969) in which the calyx lobes can vary in size and shape. The species has an impressed midvein, pubescent inflorescence, and four internally pubescent, unequal calyx lobes. McVaugh (1969) noted the similarity of this species to *M. umbraticola* in the context of the arbitrary division of closely related species into different genera according to their calyces. We are grateful to Bruce Holst (pers. comm.) who focused his attention on the morphological similarity between this species and *M. lucida*. Specimens previously attributed to *M. lucida* have particularly subcordate leaf bases and lustrous leaves, whilst the type specimen of *M. lucida* var. *attenuata* has narrower leaves with longer acumen to 2.5 cm and unusually long inflorescences to 12 cm. However, all these variable characteristics fit within the circumscription

of *M. inaequiloba* followed here, and distributions are sympatric. We interpret *M. lucida* var. *attenuata* as an attenuate local morphological extreme and synonymize both varieties of *M. lucida* under *M. inaequiloba*.

Selected specimens. BOLIVIA. **Santa Cruz:** Velasco, Parque Nacional Noel Kempff Mercado, laguna Bella Vista, R. Guillén 3817 (SEL not seen). BRAZIL. **Amazonas:** Barcelos, Margens do Rio Araca proximo Rio Januari, Cordeiro 144 (K). **Mato Grosso:** Barra do Garças, above Agua Quente, Ratter 3275 (K). **Roraima:** Rio Murupu, 28 km NW of Boa Vista, rd. to Taiano, Prance 9130 (K, U). ECUADOR. **Morona-Santiago:** Centro Shuar Yukutais, W of Pedro Kunkumas' house and S of school, Bennett 4145 (NY). FRENCH GUIANA. Piste de Saint-Elie, Sabatier 877 (CAY). GUYANA. **Potaro-Siparuni:** Kato, Potaro-Siparuni, Hahn 5610 (K). **Upper Takutu–Upper Essequibo:** Isherton, basin of Rupunini River, Smith 2479 (K). PERU **Loreto:** Maynas, Rio Yuvinetto affluent du Putumayo, territoire des indiens Secoya, Barrier 654 (K). SURINAME. **Brokopondo:** Van Bloommesteijn Lake, island E of the lake, along the banks, Bhikhi 947 (K). **Pará:** Jodensavanne–Mapanekreek area, camp 8, Elburg 9398 (K). VENEZUELA. **Bolívar:** Cedenó, vic. of Panare village of Corozal, 6 km from Maniapure, Boom 6639 (K).

46. *Myrcia induta* McVaugh, Mem. New York Bot. Gard. 18: 99. 1969. TYPE: Venezuela. Amazonas: Rio Ventuari, Serrania Paru, Rio Paru, Cano Asisa, 7 Feb. 1951, R. S. Cowan 31348 (holotype, MICH-1109509!; isotypes, F-0065500F!, NY-00564000!, VEN-75662!). [Species group B].

Habitat and distribution. *Myrcia induta* is known from mountainous ridges in Venezuela (Amazonas) at an altitude of ca. 2000 m.

IUCN Red List category. *Myrcia induta* is known only from the type collection from a relatively poorly known and collected area; we could find no additional information regarding the type locality. *Myrcia induta* is assessed as Data Deficient (DD) according to IUCN criteria (2014).

Notes. *Myrcia induta* resembles *M. caudata*; however, the former species is distinguished by its appressed, gray hairs. The inflorescence is less than 2 cm with two to five (to 10) flowers. Although the calyx lobes are free, the short inflorescence and acuminate leaves suggest McVaugh's *Marlierea* sect. *Myrciopsis*.

47. *Myrcia insignis* (McVaugh) E. Lucas & C. E. Wilson, comb. nov. Basionym: *Marlierea insignis* McVaugh, Fieldiana, Bot. 29: 176. 1956. TYPE: Colombia. Amazonas: Vaupés, 21 June 1951, R. E. Schultes 12766 (holotype, US-

00117788!; isotypes, BM-000798860!, GH-00443660!, LE!, MICH-1109603!, US-00997540!). [No species group assignment].

Habitat and distribution. *Myrcia insignis* is known from southern Venezuela and Colombia to northern Peru at an altitude of ca. 250 m.

IUCN Red List category. *Myrcia insignis* is known to us only from the type; three further authoritatively named collections are available online (TROPICOS®, 2015). Based on the resulting distribution we calculate an EOO > 170,000 km². This species is of Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia insignis* is remarkable in its large, shortly acuminate, rounded leaves with open venation; it has globose fruits covered in golden hairs arranged on short lateral inflorescences.

48. *Myrcia insularis* Gardner, London J. Bot. 1: 536. 1842. *Aulomyrcia insularis* (Gardner) O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14: 98. 1857. TYPE: [Brazil.] Rio de Janeiro: Ilha do Governador, 1836, *G. Gardner 202* (lectotype, designated here [likely holotype], BM-000953612!; isoelectotypes, K-000343449!, K-000343450!, K-000343451!, P-00161230!). [Species group A].

Aulomyrcia insularis var. *punctata* O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14: 98. 1857. TYPE: [Brazil. Pernambuco], 1838, *G. Gardner 1016* (lectotype, designated here, P-00163115!; isoelectotypes, BM-000953611!, E-00504681!, F-0064726!, F-0064730F!, G-00222233!, GH-00071103!, K-000018494!, K-000018495!, K-000342595!, NY-00386669!, P-00163113!, P-00163114!, US-00117779!).

Habitat and distribution. *Myrcia insularis* is endemic to restinga and tabuleiro vegetation of the Atlantic forests in southeastern Brazil (Bahia to Rio de Janeiro). It has been collected from altitudes of 0–100 m.

IUCN Red List category. *Myrcia insularis* is known to us from 11 collections from 10 independent localities (EOO of ca. 250,000 km²); approximately half of these are from pre-1900. This species occurs only in the most littoral part of the Atlantic forest. Although the EOO is large enough, this falls short of the IUCN criteria of threat. However, these forests are extremely pressured by sprawling residential development (Google Inc., 2015). The species is assessed as Near Threatened (NT) according to IUCN criteria (2014).

Notes. Gardner's original material of *Myrcia insularis* was collected in Rio de Janeiro from Ilha do Governador. *Gardner 202* (BM) is the only duplicate to bear this locality, and we take this to be the type. This species has decussate leaves, a flat or slightly raised midvein, free calyx lobes, and terminal, whorled, glabrous inflorescences subtended by large bracts. *Myrcia insularis* is similar to *M. hexasticha*, but we maintain the distinction between the two species as the latter has ternate leaves; both are similar to *M. obversa*, which has much larger open flowers (ca. 5 mm vs. ca. 1.5 mm in *M. insularis*) and a denser indument.

Selected specimens. BRAZIL. **Bahia:** Ilhéus, Castelo Novo, *Riedel 514* (K). **Espírito Santo:** Linhares, Res. Nat. CVRD, *Folli 4138* (K). **Rio de Janeiro:** Guanabara, Floresta de Tijuca, *Strang 543* (K).

49. *Myrcia karuaiensis* (Steyerm.) E. Lucas & C. E. Wilson, comb. nov. Basionym: *Aulomyrcia karuaiensis* Steyerm., Fieldiana, Bot. 28: 1005. 1957. *Marlierea karuaiensis* (Steyerm.) McVaugh, Mem. New York Bot. Gard. 10: 85. 1958. TYPE: [Venezuela.] Bolívar: Salto de Iraba-naima waterfall, Ptari-tepui, 28 Nov. 1944, *J. A. Steyermark 60702* (holotype, F not seen; isotypes, U-0005120!, VEN-37433!). [Species group B].

Habitat and distribution. *Myrcia karuaiensis* has been collected from Venezuela to Guyana from altitudes of 200–1000 m.

IUCN Red List category. *Myrcia karuaiensis* is known to us from five collections from four localities but is well represented in online herbaria, giving an EOO > 225,000 km². This species is relatively well and recently collected from multiple, disjunct localities, some in national parks (WDPA, 2015). The species is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. In its short, few-flowered inflorescences with sessile distal flowers, *Myrcia karuaiensis* resembles others from *Marlierea* sect. *Myrciopsis*; McVaugh (1958) placed this species here.

Selected specimen. GUYANA. **Cuyuni-Mazaruni:** Pakaraima Mtns., Karowrieng River at Maipuri Falls, *Hoffman 2961* (K).

50. *Myrcia kylistophylla* B. Holst, Selbyana 23: 154. 2002. TYPE: Venezuela. Bolívar: Cedeno, Sierra de Maigualida, 18 Nov. 1988, *O. Huber 12794* (holotype, MYF not seen; isotype, SEL-002942!). [Species group B].

Habitat and distribution. *Myrcia kylistophylla* has been found on rocky outcrops and stream sides as well as tepui summits in Venezuela from altitudes of 1900–2100 m.

IUCN Red List category. *Myrcia kylistophylla* is known only from the three collections cited in the protologue; these give an EOO of ca. 500 km², falling into the IUCN endangered category. While the localities do not fall in protected areas, threats to the summits of tepuis are currently low. The low number of localities from which *M. kylistophylla* is known, however, means that if environmental threat increased, this species would be under pressure. We assign a category of Vulnerable (VU) according to IUCN criteria (2014).

Notes. *Myrcia kylistophylla* is distinct in its strongly revolute leaves, open venation, reduced axillary inflorescences, and dense indumentum on leaves abaxially as well as on pedicels and hypanthium. Holst (2002) suggested an affinity with *M. gentryi* (from which it is distinguished by its revolute leaf margins) and other species associated here with *Marlierea* sect. *Myrciopsis* (McVaugh, 1958). A shared character among these species is the reduced nature of the inflorescence. Additional specimens are cited by Holst (2002).

51. *Myrcia liesneri* B. Holst, Selbyana 23: 154. 2002. TYPE: Venezuela. Amazonas: Rio Negro, on hills 1.5 km S of Cerro de la Neblina Base Camp, on Rio Mawarinuma, 4 Dec. 1984, R. Liesner 17494 (holotype, ASU not seen; isotypes, MO-2112609!, SEL-002943!, VEN-332431!). [Species group A].

Habitat and distribution. *Myrcia liesneri* is known from hillsides; it has been collected from Venezuelan Amazonas, at altitudes of 140–400 m.

IUCN Red List category. *Myrcia liesneri* collections are known from only the type locality and one other locale, cited in the protologue. The locations are ca. 270 km apart, hence a very restricted EOO. The collection points do not occur in any protected areas and are vulnerable to sudden stochastic events; therefore, *Myrcia liesneri* is assessed as Vulnerable (VU D2) according to IUCN criteria (2014).

Notes. *Myrcia liesneri* has a raised midvein and terminal, paired inflorescences, suggesting an affinity with similar species from the littoral forests of eastern Brazil. Leaves are subsessile and acuminate. Holst (2002) suggested an unqualified affinity to *M. revolutifolia* McVaugh from which this species is

distinguished by having more slender (2.5–3.5 times as long as wide vs. 1.5 times as long as wide) and acuminate (vs. rounded) leaves and minutely puberulent (vs. glabrous) flowers.

52. *Myrcia ligustrina* (McVaugh) E. Lucas & C. E. Wilson, comb. nov. Basionym: *Marlierea ligustrina* McVaugh, Mem. New York Bot. Gard. 10: 86. 1958. TYPE: Venezuela. Amazonas: Cerro Yapacana, Rio Orinoco, 3 Jan. 1951, B. Maguire 30738 (holotype, MICH-1109601!; isotypes, NY-00564003!, US-00117789!, VEN-41605!). [No species group assignment].

Habitat and distribution. Collections of *Myrcia ligustrina* are associated with rivers on mid- to high-altitude rocky savanna from Venezuela to Guyana, from altitudes of 550–1800 m.

IUCN Red List category. *Myrcia ligustrina* is known from four collections cited in the protologue that give an EOO of ca. 73,500 km². The relatively few, unprotected locations from which the specimens have been collected suggest a fragmented population; however, the type locality is protected in the Parque Nacional Cerro Yapacana. The species is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia ligustrina* is a species distinguished by its coriaceous leaves with raised midveins. Inflorescences are terminal and subterminal bunches of cymose panicles with flattened rachises; calyx lobes are very unequal with one often much larger than the others. McVaugh (1958) suggested a resemblance to *M. neomontana* and discusses differences in detail such as the smaller leaves with cuneate leaf bases in *M. ligustrina*.

53. *Myrcia littoralis* DC., Prodr. [de Candolle] 3: 249. 1828. TYPE: [Brazil.] in arboretis maritimis prov. Bahiensis Brasiliae, C. F. P. Martius s.n. (lectotype, designated here, M-0136953!; isotype, G-DC!). [Species group C].

Habitat and distribution. *Myrcia littoralis* is found in northeastern Brazil from Pernambuco to Bahia, in restinga vegetation at altitudes lower than 100 m.

IUCN Red List category. *Myrcia littoralis* is a common species of the Bahian restinga. Approximately 70 authoritatively named specimens are cited online (Sobral et al., 2015; speciesLink, 2015) confirming its presence in Pernambuco and Espírito

Santo and providing an EOO > 80,000 km². *Myrcia littoralis* is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia littoralis* is reminiscent, in leaf and inflorescence shape, of *M. exploratoris* and *M. coelosepala*. It differs from these latter species in its coastal distribution in restinga vegetation, its leaves that are smaller and papery (compared to those of *M. exploratoris*), and its white, silky trichomes on the inflorescences and hypanthia (vs. trichomes absent in *M. coelosepala*). *Myrcia littoralis* is a large (ca. 25 m) tree in *Myrcia* sect. *Aulomyrcia*.

Selected specimen. BRAZIL. **Bahia:** a direita de estrada principal, ca. 2 km a sul de Olivença, *Lucas 1000* (K).

54. *Myrcia lituatinervia* (O. Berg) E. Lucas & C. E. Wilson, comb. nov. Basionym: *Myrciaria lituatinervia* O. Berg, *Linnaea* 27: 322. 1856. *Marlierea lituatinervia* (O. Berg) McVaugh, *Mem. New York Bot. Gard.* 18: 65. 1969. TYPE: British Guiana. s.d., *R. Schomburgk 874* (neotype, designated by McVaugh [1969: 65], K-000261026!). [Species group B].

Habitat and distribution. *Myrcia lituatinervia* is found among rocks, from southeast Venezuela to Guyana from altitudes of ca. 500 m; the species has also been reported from Brazil.

IUCN Red List category. *Myrcia lituatinervia* is known only from the type collection and from a poorly known and collected area. This species appears to have an extremely restricted EOO and is assessed as Vulnerable (VU D2) according to IUCN criteria (2014).

Notes. *Myrcia lituatinervia* has thick, apparently fleshy pedicels and winged branchlets that “are the mark of sect. *Myrciopsis*” (McVaugh, 1969: 65). McVaugh (1969) noted a strong similarity in inflorescence and leaf disposition between *M. karuaiensis* and *M. lituatinervia*, citing a distinction based on the subcordate leaf bases in *M. lituatinervia*. Sobral et al. (2015) did not cite this species in Brazil; however, the K collection contains specimens from the Distrito Federal that match the type surprisingly well. These two specimens were the basis for the (likely mis-) naming of other specimens from Bahia and Espírito Santo as this species. This may be perpetuated in other herbaria; further study of the Distrito Federal material is required.

Selected specimen. BRAZIL. **Distrito Federal:** Brasília, Riacho Fundo, near Airport Rd., *Mendonça 144* (K).

55. *Myrcia macrocarpa* DC., *Prodr.* [de Candolle] 3: 249. 1828. *Aulomyrcia macrocarpa* (DC.) O. Berg, *Linnaea* 27: 41. 1855. TYPE: Brazil. [São Paulo:] Sebastianopolis, monte Formoso, s.d., *C. F. P. Martius s.n.* (holotype, M-0136950!; isotype, US-19816!). [No species group assignment].

Habitat and distribution. *Myrcia macrocarpa* is endemic to the mountains of Rio de Janeiro and Espírito Santo, Brazil; altitudes are not precisely known.

IUCN Red List category. Doubts regarding the specific delimitation of *Myrcia macrocarpa* require resolution before a category of threat can be assigned. The species is assessed as Data Deficient (DD) according to IUCN criteria (2014).

Notes. The type specimen of *Myrcia macrocarpa* is of a plant with a raised midvein and terminal inflorescence that otherwise resembles *M. pyrifolia*.

56. *Myrcia magna* D. Legrand, *Atas Simp. Biota Amazonica* 4: 150. 1967, replacement name. Replaced name: *Aulomyrcia grandifolia* O. Berg in C. F. P. von Martius & auct. suc. (eds.), *Fl. Bras.* 14: 97. 1857, non *Myrcia grandifolia* Cambess. in A. F. C. de Saint-Hilaire, *Fl. Bras. Merid.* 2: 298. 1832. TYPE: [Brazil.] Amazonas: Barra do Rio Negro, Oct. 1851, *R. Spruce s.n.* (holotype, M-0136853!; isotypes, F-0064722F!, G-00222416!, G-00222417!, K-000343116!, K-000343117!, K-000343961!, LE-00007074!, NY-00386668!, P-00161260!). [Species group A].

Habitat and distribution. *Myrcia magna* is known from lowland, terra firme, Amazon forest in Amazonas, Roraima, and Rondônia, at an altitude of ca. 40 m.

IUCN Red List category. *Myrcia magna* is known from ca. 12 collections available online (SpeciesLink, 2015); its EOO is > 600,000 km² but no collections are from protected areas. Lowland Amazon forest is under pressure from anthropological expansion, and, if the relatively low number of gatherings indicate a small population, *M. magna* could be at risk in the future. Without more information, however, *M. magna* is here assigned a threat category of Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia magna* has a flat to raised midvein; a terminal to subterminal pair of long (to

ca. 18 cm), lightly lanate panicles with long secondary axes; asymmetrically arranged, shortly stalked flowers; deciduous bracts; and internally glabrous calyx lobes. The species is related to those with similar gross morphology from the littoral forests of eastern Brazil, a group poorly represented in the Amazon where it may be related to *M. liesneri*.

57. *Myrcia maguirei* (McVaugh) E. Lucas & C. E. Wilson, comb. nov. Basionym: *Marlierea maguirei* McVaugh, Mem. New York Bot. Gard. 10: 87. 1958. TYPE: Venezuela. Amazonas: Cerro Yutaje, Rio Manapiare, 9 Feb. 1953, *B. Maguire 35114* (holotype, MICH-1109600!; isotype, VEN-41595!). [Species group B].

Habitat and distribution. *Myrcia maguirei* has been collected from stream beds in Venezuela from an altitude of ca. 1400 m.

IUCN Red List category. *Myrcia maguirei* is known to us only from the type, although seven further authoritatively identified collections are cited on TROPICOS® (2015). These give an EOO of ca. 1500 km². Three collections of this species are within the Orinoco-Casiquiare Biosphere Reserve (WDPA, 2015). This species is assessed as Vulnerable (VU) according to IUCN criteria (2014).

Notes. McVaugh (1958) originally assigned *Myrcia maguirei* to *Marlierea* sect. *Myrciopsis*; the rheophytic habit of the species is suggested by the plant's reduced paniculate inflorescences with rounded rachises; decussate, elliptic leaves with channeled midveins; rounded internodes; and four calyx lobes persistent on a globose fruit. The whole plant is glabrous.

58. *Myrcia mathewsiana* (O. Berg) McVaugh, Publ. Field Mus. Nat. Hist., Bot. 13(4): 646. 1958. Basionym: *Aulomyrcia mathewsiana* O. Berg, Linnaea 27: 45. 1855. TYPE: Peru. Moyobamba: Chachopayos, s.d., *A. Mathews 1453* (lectotype, designated here, W-0032470!; isotypes, BM-000953648!, BM-000953649!, F-0064740F!, K-000261042!, K-000261043!, K-000261044!, K-000330184!, K-000330185!, K-000330186!, MICH-1109826!, W-0032469!). [Species group C].

Habitat and distribution. The distribution of *Myrcia mathewsiana* extends from Peru to Bolivia (in Bolivia, by WCSP, 2015), at altitudes of 800–900 m.

IUCN Red List category. *Myrcia mathewsiana* is known to us only from the type; we cannot find evidence that the species occurs in Bolivia (WCSP, 2015). Its specific delimitation requires resolution before a category of threat can be assigned. The species is assessed as Data Deficient (DD) according to IUCN criteria (2014).

Notes. *Myrcia mathewsiana* has a puberulent hypanthium and shares many characters with *M. pubiflora*. Leaf bases tend to be cordate; apart from this, it is difficult to say how these species differ and to delimit these species and several others of the decorticans complex (Kawasaki & Holst, 1994).

59. *Myrcia mcvaughii* (B. Holst) E. Lucas & C. E. Wilson, comb. nov. *Marlierea mcvaughii* B. Holst, Selbyana 23: 147. 2002. TYPE: Venezuela. Amazonas: Rio Negro, Cano Darigua, 11 km S of San Carlos de Rio Negro, *H. Clark 8302* (holotype, MO not seen; isotypes, INPA not seen, NY-00564087!, SEL-002445!, VEN-286776!). [Species group B].

Habitat and distribution. *Myrcia mcvaughii* has been collected from the Rio Negro basin on white sand shrubby savanna in Colombia, southern Venezuela, and Brazil at altitudes of ca. 120 m.

IUCN Red List category. The nine paratypes of *Myrcia mcvaughii* cited in the protologue give an EOO for this species of ca. 65,000 km², falling within the relatively unthreatened (EOE, 2015) Negro-Branco moist forest ecoregion (WWF, 2015). *Myrcia mcvaughii* is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia mcvaughii* has somewhat cymose inflorescences with flattened rachises and leaf venation reminiscent of *Marlierea* sect. *Myrciopsis*. The calyx is fused in the bud, which is reminiscent of *Calyptranthes*. The flowers tear into two to three or four lobes, giving the uneven appearance common in *Myrcia* sect. *Aulomyrcia*, while in others on the same collection, there is a calyptra. This species emerges within the clade that corresponds to *Myrcia* sect. *Aulomyrcia* in the phylogenetic analysis of Santos (2014). Holst (2002) discusses this species in the context of perplexing intermediates between *Calyptranthes* and *Marlierea*.

Selected specimen. BRAZIL. Amazonas: São Gabriel da Cachoeira, Rio Icana, Jauacana, *Rodrigues 10822* (K).

60. *Myrcia micropetala* (Mart.) Nied., Nat. Pflanzenfam. 3(7): 76. 1893. Basionym: *Eugenia*

micropetala Mart., Flora 24 (2 Beibl.): 108. 1841. *Aulomyrcia micropetala* (Mart.) O. Berg, Linnaea 27: 56. 1855. TYPE: Brazil. [Bahia:] Ilheos [Ilheus], s.d., *B. Luschnath* 116 [herb. Martius 685] (lectotype, designated here, BR-0000005269426!; isoelectotypes, BR-0000005280353!, BR-0000005280414!, BR-0000005280681!, BR-0000005280742!, BR-0000005281015!, BR-0000005281077!, F-0065228F!, G00222241!, HAL-0082957!, HAL-089748!, JE-00004847!, JE-00004848!, K-000018502!, K-000018503!, K-000018504!, LE [6]!, M-0136936M!, M-0136937!, MICH-1109673!, NY-00404955, P-00163096!, P-00163097!, S-052465!, U-0005124!, W-0032472!). [Species group C].

Habitat and distribution. *Myrcia micropetala* is known from the ombrophilous forests of Bahia and (probably) Espírito Santo from an altitude of ca. 500 m.

IUCN Red List category. *Myrcia micropetala* is known to us from five collections with a further 10 available online (speciesLink, 2015), giving an EOO > 8000 km². The species has been found exclusively in the coastal forests of southern Bahia, a habitat under extreme pressure and threat from habitat removal and urban development. Thus, our assessment is Vulnerable (VU) according to IUCN criteria (2014).

Notes. Plants of *Myrcia micropetala* have large, somewhat bullate leaves, a conspicuously raised midvein, terminal inflorescences, large, persistent inflorescence bracts, and dense indumentum on leaves and inflorescences. The inflorescence of *M. micropetala* is typical for *Myrcia* sect. *Aulomyrcia*; however, the calyx lobes of this species are relatively small (no more than 1.5 mm) and unusually reflexed. This species is reminiscent of *M. racemosa* in its small, pubescent flowers, leaves drying green, and venation.

Selected specimen. BRAZIL. **Bahia:** Una, Res. Biol. Mico-Leão (IBAMA), entrada no Km. 46 da Rod. BA-001 Ilheus/Una, *Jardim* 1076 (K).

61. *Myrcia minutiflora* Sagot, Ann. Sci. Nat., Bot., VI, 20: 185. 1885. *Aulomyrcia minutiflora* (Sagot) Amshoff, Bull. Torrey Bot. Club 75: 532. 1948. TYPE: [French Guiana.] Maroni, 1862, *M. Melinon s.n.* (holotype, P-00163092!; isotypes, F-0065529F!, NY-00405453!, P-

00163093!, P-00163094!, P-00163095!, US-00117761!). [Species group B].

Habitat and distribution. *Myrcia minutiflora* has been collected from dense rainforest in Guyana, Suriname, and the Amazonian states of Brazil to northern Mato Grosso, from altitudes of 100–800 m.

IUCN Red List category. *Myrcia minutiflora* is known to us from ca. 40 collections from more than 30 localities, with an EOO of ca. 3 million km². This species is assessed as of Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia minutiflora* is a species distinctive in its venation that tends to be more open than usual in *Myrcia* s.l.; there is a deeply looping intra-marginal vein running to 5 mm from the edge of the leaf. The blade venation is deeply impressed adaxially, and the leaves are long-acuminate. Inflorescences are short, lateral, and in loose cymes, and fruits are on short stalks. Holst (2002) suggested an unqualified affinity with *M. bolivarensis* and provided additional specimen citations.

Selected specimens. BRAZIL. **Acre:** Cruzeiro do Sul, Estr. Alemanha, forest on terra firme, *Prance* 11853 (K). **Amazonas:** Manaus, Res. Flor. Ducke, Manaus–Itacoatiara, Km. 26, *Prance* 2156 (K). **Mato Grosso:** Novo Mundo, Parque Est. Christalino, mata proxima a estrada, *Henicka* 285 (K). **Pará:** Km. 0–1.5, line SW of Ilha de Breu, *Prance* 1376 (K). FRENCH GUIANA. Mont Belvédère de la Haute Camopi, bassin de la Camopi, *de Granville* 7171. GUYANA. Upper Takutu–Upper Essequibo, Gunn’s, Essequibo River, *Jansen-Jacobs* 1509 (K). VENEZUELA. **Amazonas:** Rio Mavaca, trail near base camp, *Beck* 911 (K).

62. *Myrcia morroqueimadensis* Kiaersk., Enum. Myrt. Bras., 73. 1893. TYPE: Brazil. Rio de Janeiro: Morro Queimado, 14 Aug. 1873, A. F. M. *Glaziou* 6537 (lectotype, designated here [likely holotype], C-10015873!; isoelectotypes, K-000343766!, LE-00007194!, P-00161210!, P-00161211!, R-000009032!). [Species group C].

Habitat and distribution. *Myrcia morroqueimadensis* is recorded from the moist forests of the hills of Rio de Janeiro and Espírito Santo at altitudes of 500–950 m.

IUCN Red List category. *Myrcia morroqueimadensis* is known to us from the type collection and four other authoratively named collections available via SpeciesLink (2015). These indicate an EOO of < 5000 km² and a small population; the forests on the Atlantic coast of Brazil are under extreme anthropo-

logical pressure. We assign a threat category of Endangered (EN) according to IUCN criteria (2014).

Notes. *Myrcia morroqueimadensis* resembles species with elliptic-obovate leaves and open venation such as *M. coelosepala* and *M. littoralis*. The former species is unique in its thickened, hairy staminal disk and large buds, both unusual characters for *Myrcia* sect. *Aulomyrcia*.

63. *Myrcia multiflora* (Lam.) DC., Prodr. [de Candolle] 3: 244. 1828. Basionym: *Eugenia multiflora* Lam., Encycl. 3: 202. 1789. *Myrtus multiflora* (Lam.) Spreng., Syst. Veg. 2: 485. 1825. *Cumetea multiflora* (Lam.) Raf., Sylva Tellur., 106. 1838. *Aulomyrcia multiflora* (Lam.) O. Berg, Linnaea 27 (1): 47. 1855. TYPE: French Guiana. Cayenne, s.d., *M. Stoupy* s.n. [herb. Lamarck?] (holotype, Hb. Lamarck, not located). [Species group C].

Myrcia heringeriana Mattos, Loefgrenia 126: 2. 2008, syn. nov. *Aulomyrcia goyazensis* O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14(1): 85. 1857. TYPE: [Brazil.] Goyaz, s.d., *G. Gardner 3184*, p.p. (lectotype, designated here, W-0032608!; isolectotypes, BM!, K-000304987!, K-000304986!, NY-00386667!, P-05262210!, P-05262214!, W-18890116269!).

Myrcia pallida (O. Berg) N. Silveira, Loefgrenia 88: 2. 1985, syn. nov. *Aulomyrcia pallida* O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14(1): 87. 1857. TYPE: [Brazil.] Arrayal Porto Real, in prov. Goyaz, s.d., *J. B. E. Pohl 1061* (lectotype, designated here, W-0037068!; isolectotypes, K-000331535!, K-000344040!, W-0037067!).

Myrcia taubatensis Kiaersk., Enum. Myrt. Bras., 79. 1893, syn. nov. *Aulomyrcia buxifolia* O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14(1): 80. 1857. TYPE: [Brazil.] Serra do Sucuriuh in Minas Novas, s.d., *J. B. E. Pohl 1087*, p.p. (lectotype, designated here, BR-0000005238361!).

Habitat and distribution. *Myrcia multiflora* is distributed from Trinidad to tropical South America at altitudes of 5–3000 m.

IUCN Red List category. *Myrcia multiflora* is an extremely widespread species with an EOO > 11 million km². *Myrcia multiflora* is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. As transferred by Berg (1855–1856), this species differs from other *Aulomyrcia* species in having regularly branching axillary panicles without persistent bracts. The molecular analysis of Lucas et al. (2011) placed *Myrcia multiflora* in the *Aulomyrcia* clade; the bilocular ovary and extended hypanthium of *M. multiflora* support that placement. In its small leaves that tend to dry green, the species is

sometimes confused with *M. laruotteana* Cambess. and allied species (not treated here); however, the calyx lobes of *M. multiflora* are held upright and never sharply reflexed as in *M. laruotteana*. The bud is constricted above the ovary in *M. laruotteana* and allied species; this is not the case in *M. multiflora*. No herbarium is cited in the protologue, and the type specimen has not been located at P or in the online herbarium of Lamarck (Corsi, 2012), where it is believed to be, with the rest of Lamarck's original material. Until the Lamarck collection is physically checked, we do not consider neotypification. The typification of *A. goyazensis* is complicated by a numbering error that is described by Hochreuter on the NY isolectotype; that label suggests that while *Gardner 3184* is cited in the protologue, a correction “in the copy of Kew HB” (not found) is evidence that the type number is 3186. Study has found sheets of apparently the same collection marked 3184 or 3186; the W lectotype bears 3184 with a loose label marked 3186. The problem may be due to an orthographic misinterpretation of the “4” for a “6” as they have similar formation on some sheets. This is further complicated as Gardner sheets of a gathering of *Psidium riparium* Mart. ex DC. numbered 3184 exist at W and G; we assume these to have been misnumbered. However, if the type was supposed to be 3186, these sheets may represent the original 3184. As it is we assume the type of *A. goyazensis* to be *Gardner 3184* and a mixed gathering, hence its citation pro parte. The lectotypification of *A. buxifolia* is only slightly less complicated. In the protologue, Berg described two varieties; the first, *A. buxifolia* var. *elliptica* O. Berg, matches the specific description closely and is assumed to be typical. Various duplicates of the *Pohl 1087* type gathering exist but only that at M bears “var. *elliptica*,” consistent with Berg having seen it in Martius's herbarium; this gathering is also cited pro parte.

Selected specimens. ARGENTINA. **Buenos Aires:** *Parodi 128* (K). BOLIVIA. **Beni:** 157 km de El Mirador hacia Riberalta, 4 km desoues del desvio a Cobija, *de Michel 2070* (K). **Cochabamba:** Chapare, 1 km Agrigento B, Villa Tunari, *Wood 11508* (K). BRAZIL. **Amapá:** Rio Oiapoque Roche Mon Pere, *Irwin 48642* (K). **Bahia:** Serra Grande, estr. Serra Grande–Ilhéus, *Amorim 355* (K). **Ceara:** Crato, Floresta Nac. Araripe, *Simon 219* (K). **Espírito Santo:** Est. Biol. Santa Lúcia, *Thomaz 1392* (K); Res. Comp. Vale do Rio Doce, estr. Mantegueira, *Lucas 824* (K). **Goíás:** Serra do Caiapo, 40 km S of Caiponia, *Prance 59568* (K); Corrego Lajeadao, faz. Bandeirante, 45 km from Doverlandia on rd. to Baliza, *Ratter 7389* (K). **Maranhão:** Caxias, along BR 316 betw. Caxias & Timon, 39 km SE of Caxias & ca. 37 km NW of Teresina, *Thomas 4197* (NY); Maracassume River region, Campode Boa Esperanca, *Froes 2003* (K). **Mato Grosso:** Sinop & Colider, along BR 080, 65 km E of jct. with BR 163, *Thomas 4197* (K). **Minas Gerais:** Parque

Nat. Caraca, *Mazine* 853 (K); Itatiaia, margem da restinga do Ribeirao da Cachoeira, *Peron* 517 (K). **Pará:** Serra dos Carajas, Serra Norte, 25 km E of AMZA Expl. Camp, *Berg* 569 (K); Serra do Cachorro, *Cid Ferreira* 9710 (K). **Paraná:** Sete Quadras, *Hatschbach* 10505 (K). **Piauí:** estr. para Piracuruca entrada a direita ca. 10 km na estrada depois de Brazileira, *Nascimento* 442 (K). **Rio de Janeiro:** Saquarema, estr. Pará–Praia Grande, Saquarema–Restinga, *Sucre* 11365 (K). **Rio Grande do Norte:** São José de Mipibu, Terras do Engenho Taborda, 12 Jan. 1965, *S. Tavares s.n.* (NY). **Rondônia:** 15 km E of 117 km, *Prance* 6876 (K). **Santa Catarina:** Pinhal de Cia, Lauro Muller–Urucanga, *Reitz* 8508 (K). **São Paulo:** faz. Barreiro Rico, *Cesar* 2349 (K); ca. 10 km da cicade em direcao a Lençóis, prox. entrada da faz. Agua do Bugre, *Souza* 9566 (K). **Sergipe:** Estância, Rod. Estância/Abais, com entrada no Km. 11 da Rod. BR 101 (trecho Estância/Aracajú) 20 km ao leste do entrocamento, *Silva* 3015 (NY). FRENCH GUIANA. Pointe Kanawa–Awala-Yalimapo, Région littorale, *de Granville* 135471 (CAY). GUYANA. Upper Takutu–Upper Essequibo, Acarai Mtns., summit & adjaent slopes of Tinarnau Peak, *Henkel* 4984 (NY). PARAGUAY. **Alto Paraguay:** Alto Paraná, *Fiebrig* 6334 (K). TRINIDAD AND TOBAGO. St. George, Piarco, S of Arouca, *Britton* 94 (K). VENEZUELA. **Bolívar:** Represa Guri, ca. 0.5 km SSW of dam, *Liesner* 11040 (NY).

- 64. *Myrcia multiglomerata*** (Amshoff) E. Lucas & C. E. Wilson, comb. nov. Basionym: *Marlierea multiglomerata* Amshoff, *Recueil Trav. Bot. Néerl.* 42: 3. 1950. TYPE: Suriname. Marowijne River, 1861, *A. Kappler* 100 (holotype, U-0008498!). [Species group B].

Habitat and distribution. *Myrcia multiglomerata* is endemic to the Marowijne River region of French Guiana and Suriname; its precise altitude is unknown.

IUCN Red List category. *Myrcia multiglomerata* is known to us from six collections. The exact locality of the type collection is unknown and the EOO is < 10 km². This suggests a conservation status of critically endangered, which is supported by the low number of locations from which it has been collected and threats to the area from anthropogenic activity, e.g., mining and agriculture (EOE, 2015), which put local endemics at risk. It is assessed as Critically Endangered (CR) according to IUCN criteria (2014).

Notes. *Myrcia multiglomerata* has shortened, lateral inflorescences and glomerate flowers, and resembles those grouped by McVaugh (1958) in his *Marlierea* sect. *Myrciopsis*. Amshoff (1950) compares *M. multiglomerata* to *M. guildingiana*, but in the latter species the inflorescence is glabrous and flower buds open at the apex.

Selected specimen. FRENCH GUIANA. Village Wayampi de Trois-Sauts, Bassin de l'Oyapock, *Grenand* 551 (CAY).

- 65. *Myrcia myriantha*** McVaugh, *Mem. New York Bot. Gard.* 18: 116. 1969. TYPE: [Guyana.] Upper Mazaruni River basin: Mt. Ayanganna, NE side, 3 Aug. 1960, *S. S. Tillett* 45013 (holotype, MICH-1109501!; isotypes, F-0065532F!, NY-00405455!, S-052466!, US-00117762!, VEN-75711!). [No species group assignment].

Habitat and distribution. *Myrcia myriantha* is known from the mixed evergreen forests of Guyana at an altitude of ca. 750 m.

IUCN Red List category. *Myrcia myriantha* is known only from the type, hence a very restricted AOO. It is found in an area under threat from low-level anthropogenic activity, e.g., mining and agriculture (EOE, 2015), which puts local endemics at risk. *Myrcia myriantha* is assessed as Vulnerable (VU D2) according to IUCN criteria (2014).

Notes. McVaugh (1969) noted that *Myrcia myriantha* has unisexual flowers; no female flowers have been observed, so the number of locules is unknown. The species has relatively large leaves (to 15 cm), an impressed midvein, and lobes that do not tear. Buds are arranged in tight bunches in well-developed, somewhat asymmetric panicles; small, pointed bracts persist at the bases of terminal rachises. For now we follow McVaugh (1969) in placing this species in *Aulomyrcia*.

- 66. *Myrcia myrtilifolia*** DC., *Prodr.* [de Candolle] 3: 250. 1828. TYPE: [Brazil.] prov. Bahia, s.d., *C. F. P. Martius s.n.* (lectotype, designated here, M-0136931!; isoelectotypes, G-DC!, M-0136931!). [Species group C].

Myrcia dictyophylla (O. Berg) Mattos & D. Legrand, *Loefgrenia* 67: 5. 1975, syn. nov. *Aulomyrcia dictyophylla* O. Berg in C. F. P. von Martius & auct. suc. (eds.), *Fl. Bras.* 14(1): 72. 1857. TYPE: [Brazil.] Minas Gerais: Cachoeira do campo, s.d., *J. B. E. Pohl* 2146 (holotype, W-0040183!).

Myrcia parnajibensis (O. Berg) Kiaersk., *Enum. Myrt. Bras.*, 89. 1893, syn. nov. *Aulomyrcia parnajibensis* O. Berg in C. F. P. von Martius & auct. suc. (eds.), *Fl. Bras.* 14(1): 135. 1857. TYPE: [Brazil.] Ad flumen Parnahiba in prov. Goyaz, s.d., *J. B. E. Pohl* 544 (holotype, W-0048299!).

Myrcia rorida (O. Berg) Kiaersk., *Enum. Myrt. Bras.*, 79. 1893, syn. nov. *Aulomyrcia rorida* O. Berg in Mart., *Fl. Bras.* 14(1): 552. 1859. TYPE: [Brazil.] Rio de S. Marcos prov. Goyazensis, Aug. 1834, *L. Riedel* 2491 (lectotype, designated here, WRchb18890100483!;

isolectotypes, F-0064764F!, K-000261557!, M-0137034!, P-00161108!, P-00161109!, S-052504!, U-0005141!, W-0033240!).

Myrcia rubella Cambess. in A. St.-Hil., Fl. Bras. Merid. 2: 317. 1832, syn. nov. TYPE: [Brazil.] provinciae Goyaz, s.d., A. F. C. de Saint-Hilaire 859 (lectotype, designated here, MPU-010962!; isolectotypes, F-0065562F!, P-00161375!, P-00161376!, P-00161377!).

Habitat and distribution. *Myrcia myrtillifolia* occurs in Bolivia and is common in central and western Brazil from Tocantins and Bahia to Mato Grosso, in cerrado and cerrado rupestre vegetation from 300 to 1100 m.

IUCN Red List category. *Myrcia myrtillifolia* is a relatively common species found throughout Central Brazil and has an EOO > 1,200,000 km². *Myrcia myrtillifolia* is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. Berg (1857–1859) cited *Myrcia myrtillifolia* from Rio de Janeiro; this was based on a St. Hilaire collection in Paris that is not conspecific with the type. *Myrcia myrtillifolia* and its synonyms were until very recently considered synonymous with the non-*Myrcia* sect. *Aulomyrcia* species *M. guianensis*. The extensive new synonymy presented here reflects this radical new arrangement. In this sense, *M. myrtillifolia* varies from a tree to a suffrutex and encompasses narrowly elliptic or elliptic-ovate to obovate leaves. Character variation is markedly continuous with all habits found throughout its range. The species is recognized by its sessile leaves or with very short, pinkish petioles; new growth can be lightly pubescent, but the plant is usually glabrous. The adaxial midvein is channeled from the petiole to the center of the leaf, after which it is flat. Venation is reticulate and leaves usually dry pale green. Flower buds and inflorescence rachises are often pink-tinged; inflorescences are markedly delicate. No material of *Aulomyrcia rorida* was found in LE despite its citation in the protologue, and the specimen from W-Rehb was therefore selected. Examination of the type of *A. parnajibensis* in W found the species to be bilocular, despite it being recorded with three locules in the protologue. Sobral (2010) reduced *M. paracatuensis* Kiaersk. into the synonymy of *M. parnajibensis* likely due to this confusion regarding locules and leaf similarity; the former species is trilocular and belongs to the clade in which *M. guianensis* occurs (Lima, in prep.).

Selected specimens. BOLIVIA. **Santa Cruz:** Velasco, Parque Nacional Noel Kempff Mercado, Serrania de

Huanchaca, Wood 25206 (K). BRAZIL. **Distrito Federal:** Brasília, Fazenda Água Limpa na UnB próximo ao Centro de Primatologia, Soares-Silva 751 (K). **Goiás:** Pirenópolis, Serra dos Pirineus a 6 km em direção ao Parque Estadual dos Pirineus, Monteiro 105 (K). **Mato Grosso:** Serra do Garças, Pé da Serra, terreno arenoso, Onishi 1078 (K). **Minas Gerais:** Capitólio, Estrada para Paraíso Perdido, Lima 474 (K); Uberlândia, Reserva Ecológica do Clube Caça e Pesca, Lima 381 (K). **Tocantins:** 69 km from Porto Natl. on the rd. to Ponte Alta, Bridgewater 1076 (K).

67. *Myrcia neobuxifolia* E. Lucas & C. E. Wilson, nom. nov. Replaced name: *Marlierea buxifolia* Amshoff, Bull. Torrey Bot. Club 75: 529. 1948, non *Myrcia buxifolia* Gardner, London J. Bot. 4: 101. 1845. TYPE: [Guyana.] Kaieteur savanna, 4 Sep. 1937, C. I. Sandwith 1340 (holotype, U-0102925!; isotypes, K-000330683!, K-000330684!, NY-00405290!, U-0102925). [No species group assignment].

Habitat and distribution. *Myrcia neobuxifolia* is found in savanna thickets, on rocky ground from Venezuela to Guyana at altitudes of ca. 400–1300 m.

IUCN Red List category. *Myrcia neobuxifolia* has an EOO > 60,000 km², which removes it from an IUCN category of threat. However, we are only aware of seven collections from four distinct localities, suggesting the species is rare. The areas from which this species is known are not under specific threat, but low-level pressures from habitat removal for agriculture and mining are constant. This species is assessed as Near Threatened (NT) according to IUCN criteria (2014).

Notes. *Myrcia neobuxifolia* is a distinctive species with small, rounded leaves and reduced inflorescences; the whole plant is pubescent with white hairs on the inflorescence and young growth turning black with age.

Selected specimens. GUYANA. Wenamu trail, Parima savanna, 6 Nov. 1966, Forest Department of British Guiana 167 (K). VENEZUELA. **Bolívar:** Formacio Roraima, en Rio Cutuni, Km. 130–131 S de El Dorado, Steyermark 104079 (K).

68. *Myrcia neocuprea* E. Lucas & C. E. Wilson, nom. nov. Replaced name: *Marlierea cuprea* Amshoff, Bull. Torrey Bot. Club 75: 530. 1948, non *Myrcia cuprea* (O. Berg) Kiaersk., Enum. Myrt. Bras. 95. 1893. TYPE: [Guyana.] Kurupung; Upper Mazaruni River, s.d., H. Leng 298 (lectotype, designated here [likely holotype], NY-00405293!). [Species group C].

Habitat and distribution. *Myrcia neocuprea* is found in Venezuela, Guyana, Suriname, and French Guiana, along rivers at an altitude of ca. 100 m.

IUCN Red List category. *Myrcia neocuprea* is known to us from six collections, with an EOO of > 50,000 km². This species has a large but fragmented range; the area is under threat from low-level habitat removal from a variety of sources such as mining and agriculture. This species is assessed as Near Threatened (NT) according to IUCN criteria (2014).

Notes. *Myrcia neocuprea* has an impressed mid-vein on adaxial blades and lightly corky petioles, which places it in the decorticans complex of Kawasaki and Holst (1994). *Myrcia neocuprea* is distinctive in its long panicles with persistent bracts and whiplike branchlets covered in red hairs. Flowers tear into four or five very unequal-sized, internally pubescent calyx lobes. Holst (2002) provided further description and suggested an affinity to *M. decorticans* based on shared leaf texture and rimose petioles.

Selected specimens. FRENCH GUIANA. Riviere Arataye, Saut Pararé, *Sastre* 5846 (K). GUYANA. Along Mazaruni River, confluence with Kamarang River, Cuyuni-Mazaruni, *McDowell* 2557 (CAY).

69. *Myrcia neodimorpha* E. Lucas & C. E. Wilson, nom. nov. Replaced name: *Marlierea dimorpha* O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14(1): 538. 1859, non *Myrcia dimorpha* (O. Berg) N. Silveira, *Loefgrenia* 88: 1. 1985. TYPE: [Brazil.] Goiatacazes, Lagoa Fria, 1833, *L. Riedel* [341] (lectotype, designated here, LE-00004017!; isoelectotypes, G-00223338!, K-000330498!, LE [2]!). [Species group E].

Habitat and distribution. *Myrcia neodimorpha* is distributed in the littoral rainforests of eastern Brazil from Espírito Santo to northern Rio de Janeiro and is found at altitudes of ca. 15–50 m.

IUCN Red List category. *Myrcia neodimorpha* is known to us from four collections. This species has an EOO of ca. 1500 km² in a biome under acute environmental threat. *Myrcia neodimorpha* is assessed as Endangered (EN) according to IUCN criteria (2014).

Notes. *Myrcia neodimorpha* has large bracts subtending the secondary branchlets of the inflorescence; these bracts resemble leaves and can be present elsewhere other than on the inflorescence, giving the impression that leaves are dimorphic. In

the study of Santos (2014), this species emerges in a clade with *M. amazonica*. The type does not bear resemblance to the latter species; further investigation is required.

Selected specimen. BRAZIL. **Espírito Santo:** Praia de Maroba, *Matsumoto* 828 (K, UEC).

70. *Myrcia neoestrellensis* E. Lucas & C. E. Wilson, nom. nov. Replaced name: *Marlierea estrellensis* O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14: 34. 1857, non *Myrcia estrellensis* Kiaersk., Enum. Myrt. Bras., 107. 1893. TYPE: [Brazil. São Paulo:] Serra d'Estrela, Corrego Secco, s.d., *H. Beyrich* s.n. (holotype, B†; lectotype, designated here, illustration from Fl. Bras. 14: tab 14. 1857!). [Species group A].

Habitat and distribution. *Myrcia neoestrellensis* occurs in the coastal cordillera of the Atlantic forests of southeastern Brazil at an altitude of ca. 500 m.

IUCN Red List category. *Myrcia neoestrellensis* is known from the type collection as well as a single gathering from Espírito Santo. The species has a restricted distribution and is evidently rare; it occurs in an environment under acute threat but has been collected recently in the Linhares forest reserve. If this protection was removed, the species would be endangered. *Myrcia neoestrellensis* is assessed as Near Threatened (NT) according to IUCN criteria (2014).

Notes. The illustration (tab. 14) in *Flora Brasiliensis* provides a clear concept of *Myrcia neoestrellensis*. While the modern collection cited here matches this image well, we believe the image conveys Berg's concept more reliably and designate it as the lectotype.

Selected specimen. BRAZIL. **Espírito Santo:** Linhares, Reserva Florestal da CVRD, Estr. Gávea, antiga X-2, Km. 19868, lado esquerdo, *Folli* 319 (CVRD).

71. *Myrcia neoglabra* E. Lucas & C. E. Wilson, nom. nov. Replaced name: *Marlierea glabra* Cambess., Fl. Bras. Merid. 2: 374. 1833, non *Myrcia glabra* (O. Berg) D. Legrand, *Sellowia* 13: 298. 1961. TYPE: Brazil. Sebastianopolis, s.d., *A. F. C. de Saint-Hilaire* s.n. (lectotype, designated here [likely holotype], MPU-010972!; isoelectotypes, P-00217941!, P-00217942!, P-00217943!). [Species group E].

Marlierea grandifolia O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14: 37. 1857. TYPE: [Brazil.] Brasilia oriental, s.d., *F. C. Raben* 798 (lectotype, designated here [likely holotype], BR-0000008455215!).

Marlierea schottiana O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14: 36. 1857. TYPE: [Brazil.] Rio de Janeiro, s.d., *H. W. Schott 1042* (lectotype, designated here [likely holotype], W-0037116!; isolectotypes, BR-0000008452009!, K-000330499!, K-000330500!, W-0037114!, W-0037115!).

Habitat and distribution. *Myrcia neoglabra* is found in the Brazilian Atlantic forests from southern Bahia to Rio de Janeiro at altitudes of ca. 0–150 m.

IUCN Red List category. *Myrcia neoglabra* is known to us from 10 collections from 10 localities. A distribution from Bahia to Rio de Janeiro supports an EOO of > 100,000 km². Although this EOO prevents assigning a category of threat, the species has not been frequently collected, suggesting it is rare. It has not been collected from protected areas, and threats to the Atlantic rainforest are acute. *Myrcia neoglabra* is assessed as Near Threatened (NT) according to IUCN criteria (2014).

Notes. *Myrcia neoglabra* has raised midveins on adaxial blade surfaces and whorled inflorescences; it can also have cordate or cuneate leaf bases and thickened petioles.

Selected specimens. BRAZIL. **Bahia:** Ilhéus, Faz. Barra do Manguiho, *Mattos Silva 2028* (K). **Espírito Santo:** Reserva Flor. Linhares CVRD, *Lino 78* (K). **Rio de Janeiro:** Corcovado, Caixa d'Água, *Glaziou 4813* (K).

72. *Myrcia neoimperfecta* E. Lucas & C. E. Wilson, nom. nov. Replaced name: *Marlierea imperfecta* McVaugh, Fieldiana, Bot. 29: 176. 1956, non *Myrcia imperfecta* McVaugh, Mem. New York Bot. Gard. 18(2): 95. 1969. TYPE: Peru. Loreto: Mishuyacu, near Iquitos, Jan. 1930, *G. Klug 787* (holotype, US-00117787!; isotypes, F-0040041F!, NY-00405296!). [No species group assignment].

Habitat and distribution. *Myrcia neoimperfecta* is endemic to the wet forests of Peru at an altitude of ca. 100 m.

IUCN Red List category. *Myrcia neoimperfecta* is known to us only from the type; four further authoritatively named collections on TROPICOS® (2015) indicate an EOO of ca. 750 km², centered around Iquitos. It has been assessed by Bocángel et al. (2006) to be Endangered (EN) according to IUCN criteria (2014).

Notes. The species is characterized by three times branching, somewhat cymosely branching panicles to 14 cm, impressed midveins, and relatively

large, acuminate leaves to 25 cm. Flower buds are completely closed, and rachises of the inflorescence are flattened. The large leaves are reminiscent of *M. neomacrophylla* E. Lucas & C. E. Wilson.

73. *Myrcia neomacrophylla* E. Lucas & C. E. Wilson, nom. nov. Replaced name: *Marlierea macrophylla* Amshoff, Recueil Trav. Bot. Néerl. 42: 2. 1950, non *Myrcia macrophylla* DC., Prodr. [de Candolle] 3: 247. 1828. TYPE: British Guiana. 107 m, Bartica–Potaro Rd., 12 Nov. 1943, *D. B. Fanshawe 1454* [Forest Dept. 4190] (lectotype, designated here, K-000261028!; isolectotype, NY-00405298!). [No species group assignment].

Habitat and distribution. *Myrcia neomacrophylla* is found in forest on lateritic soil in Guyana; it is also reported from Venezuela at an altitude of ca. 100 m.

IUCN Red List category. *Myrcia neomacrophylla* is known to us from three collections from three localities with an EOO of ca. 2000 km². *Myrcia neomacrophylla* is assessed as Endangered (EN) according to IUCN criteria (2014).

Notes. *Myrcia neomacrophylla* has long, terminal inflorescences with acutely flattened axes and a flat or slightly channeled midvein. Amshoff noted a similarity with Brazilian *M. neoverticillaris* but indicates larger flowers and non-verticillate leaves in *M. neomacrophylla*. The distinctive flattened inflorescence axes of the type of *M. neomacrophylla* are not shared by *M. neoverticillaris*; *M. neomacrophylla* also has completely closed buds. In these respects, *M. neomacrophylla* resembles *M. neoimperfecta*. TROPICOS® (2015) cited a specimen from Venezuela with no further details.

Selected specimen. GUYANA. **Potaro-Siparuni:** Eagle Mtn., *Fanshawe 1126* [Forest Dept. 3862] (K).

74. *Myrcia neomontana* E. Lucas & C. E. Wilson, nom. nov. Replaced name: *Eugenia montana* Aubl., Hist. Pl. Guiane 1: 495. 1775, non *Myrcia montana* Cambess., Fl. Bras. Merid. (A. St.-Hil.) [quarto ed.] 2(19): 325. 1829 [1832]. *Cumetea montana* (Aubl.) Raf., Sylva Tellur., 106. 1838. *Marlierea montana* (Aubl.) Amshoff, Recueil Trav. Bot. Néerl. 39: 147. 1942. *Myrcianthes montana* (Aubl.) C. Nelson, Anales Jard. Bot. Madrid 57: 406. 1999 [2000]. TYPE: French Guiana. Lupra montem Serpent dictum, 1775, *J. B. C. F. Aublet s.n.* (holotype, BM-000754877!). [No species group assignment].

Habitat and distribution. *Myrcia neomontana* is frequent in northern South America at altitudes of ca. 1000–1400 m.

IUCN Red List category. *Myrcia neomontana* is known to us from 40 collections and is very well represented in online herbaria; this common and widespread species (EOO > 1 million km²) does not qualify for an IUCN environmental threat category. *Myrcia neomontana* is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia neomontana* is a common and widespread species distinctive in its rounded, sessile to subsessile leaves and cymose, symmetrical inflorescences terminating in neat dichasia. The dichasial flowers and markedly reflexed calyx lobes are reminiscent of *Myrcianthes* O. Berg and *Myrcia tomentosa* (Aubl.) DC., respectively. The species is bilocular with an extended, tearing hypanthium. Molecular analyses (Staggemeier et al., 2015) confirm this species in *Myrcia* sect. *Aulomyrcia*.

Selected specimens. COLOMBIA. **Vaupés:** Mitu & vic., along rd. from town, *Zarucchi 1586* (K). FRENCH GUIANA. Piste de Saint-Elie, *Prévost 1635* (CAY). GUYANA. E Berbice-Corentyne, Thomson farm, S of Timehri, *Maas 3603* (K); Pakaraima Mtns., Imbaimadai Creek, W of Imbaima, Mazaruni-Potaro, *Pipoly 7971* (CAY). SURINAME. **Marowijne:** via secte ab Moengo tapoe ad Grote Zwiebelzwamp, *Lanjouw 886* (K). **Sipaliwini:** Tafelberg (Table Mtn.), *Maguire 24693* (K). VENEZUELA. **Amazonas:** Cerro Yapacana, *Steyermark 103122* (K).

75. *Myrcia neoobscura* E. Lucas & C. E. Wilson, nom. nov. Replaced name: *Marlierea obscura* O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14: 36. 1857, non *Myrcia obscura* (O. Berg) N. Silveira, Roessleria 7(1): 66. 1985. TYPE: [Brazil.] Minas Gerais: Presidio de S. João-Baptista, s.d., *F. Sellow s.n.* (holotype, B†; lectotype, designated here, BR-0000008455635!; isoelectotypes, K-000170002!, LE!, US-00169640!). [Species group E].

Habitat and distribution. *Myrcia neoobscura* is distributed in the Atlantic forests and campos rupestres of Bahia and Minas Gerais, Brazil, at altitudes of 1200–1500 m.

IUCN Red List category. *Myrcia neoobscura* is known to us from 11 collections representing an EOO > 130,000 km². *Myrcia neoobscura* is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia neoobscura* is a common species characterized by gray, glaucous, chartaceous leaves, a lack of indumentum, a raised midvein, and peeling bark.

Selected specimens. BRAZIL. **Bahia:** Abaíra, Bem Querer, *Nic Lughadha 50207* (K). **Minas Gerais:** Ouro Preto, Est. Ecol. Tripui, *Peron 457* (K).

76. *Myrcia neoregeliana* E. Lucas & C. E. Wilson, nom. nov. Replaced name: *Marlierea regeliana* O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14: 537. 1859, non *Myrcia regeliana* O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14: 562. 1859. TYPE: [Brazil.] s.d., *L. Riedel & Langsdorff 785* (lectotype, designated here, LE-00004037!; isoelectotypes, K-000330488!, LE [3]!, P-01902221!, W-18900002612!). [Species group E].

Habitat and distribution. *Myrcia neoregeliana* occurs in primary and secondary Atlantic rainforests of eastern Brazil, from Bahia to Santa Catarina at altitudes of ca. 15–50 m.

IUCN Red List category. *Myrcia neoregeliana* is known to us from 14 collections and is well represented in online herbaria. This relatively common and widespread species (EOO > 400,000 km²) does not qualify for an IUCN environmental threat category. *Myrcia neoregeliana* is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. The type of *Myrcia neoregeliana* is glabrous but bears resemblance to *M. neoriedeliana*. *Marlierea regeliana* var. *parviflora* Kiaersk. is densely pubescent and is synonymized in *Myrcia neoriedeliana* here. Of the four sheets at LE, only one bears the names Riedel and Langsdorff. The remaining sheets at LE, K, and W bear the name Riedel, are morphologically very similar, and are assumed to be from the same collection.

Selected specimens. BRAZIL. **Bahia:** Ilhéus, area do CEPEC, *Hage 2230* (K). **Distrito Federal:** Cotia, *Pereira 4224* (K). **Espírito Santo:** Reserva CVRD, Estr. Cainga, *Matsumoto 821* (K). **Rio de Janeiro:** Paratinuirim, estrada par leva, *Jacques 90* (K). **Santa Catarina:** Itajaí, Cunhas, *Reitz 1894* (NY).

77. *Myrcia neoriedeliana* E. Lucas & C. E. Wilson, nom. nov. Replaced name: *Eugeniopsis riedeliana* O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14: 561. 1859, non *Myrcia riedeliana* O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14(1): 565. 1859. *Marlierea riedeliana* (O. Berg) D. Legrand,

Comun. Bot. Mus. Hist. Nat. Montevideo 3(40): 31. 1962. TYPE: [Brazil.] Ilheos [Iheus]: Castel, Bahia, s.d., *L. Riedel & Langsdorff 415* (lectotype, designated here, LE-00004040!; isoelectotype, LE!). [Species group E].

Marlierea regeliana O. Berg var. *parviflora* Kiaersk., Enum. Myrt. Bras., 44. 1893, syn. nov. TYPE: [Brazil.] Rio de Janeiro, Nov. 1879, *A. F. M. Glaziou 10787* (lectotype, designated here, C-10015782!; isoelectotypes, C-10015783!, G-00359530!, K-000330489!, LE!, R-000008937!).

Habitat and distribution. *Myrcia neoriedeliana* occurs in primary and secondary Atlantic rainforests of eastern Brazil, from Bahia to Santa Catarina at altitudes of 50–1075 m.

IUCN Red List category. *Myrcia neoriedeliana* is a widespread (EOO > 200,000 km²) and relatively well-collected species from a biome under acute environmental threat. *Myrcia neoriedeliana* is assessed as Near Threatened (NT) according to IUCN criteria (2014).

Notes. Specimens of *Myrcia neoriedeliana* in widespread herbaria have been given the name *Marlierea obscura*, apparently misapplied. *Myrcia neoriedeliana* has a sunken midrib with a whorled, terminal inflorescence reminiscent of *M. amazonica*; *M. neoriedeliana* is distinguished from *M. amazonica* by its consistently larger leaves and distinctively shaggy indumentum on new growth and the underside of the midrib. Specimens from Santa Catarina at Kew are particularly endowed with indument; after close analysis, we include them and extend the species range. Berg cited unnumbered Riedel material from LE where two sheets collected by Riedel and Langsdorff were found; these match the protologue well, bear Berg's handwriting, and are assumed to be the type material.

Selected specimens. BRAZIL. **Paraná:** Alexandra, *Dusén 8319* (K). **Rio de Janeiro:** Silva Jardim, Reserva Biol. Poço das Antas, *Guedes 2284* (K). **Santa Catarina:** Itajaí, Morro da Fazenda, *Klein 1216* (K). **São Paulo:** Cunha, Parque Est. Serra do Mar, trilha do Rio Bonito, próx. da sede, *Lucas 403* (K).

78. *Myrcia neurostrata* Sobral, Novon 16: 136. 2006. Replaced name: *Aulomyrcia rostrata* O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14: 544. 1859, non *Myrcia rostrata* DC., Prodr. [de Candolle] 3: 325. 1828. TYPE: [Brazil.] Bahia, s.d., *R. Blanchet 1880* (lectotype, designated here, LE!). [No species group assignment].

Habitat and distribution. *Myrcia neurostrata* is known from the moist forests of eastern Brazil in Bahia and is likely to also occur in Espírito Santo; its altitude is not precisely known.

IUCN Red List category. *Myrcia neurostrata* is known only from the type from an unspecified locality. *Myrcia neurostrata* is assessed as Data Deficient (DD) according to IUCN criteria (2014).

Notes. The type of *Myrcia neurostrata* has chartaceous, green young leaves reminiscent of *M. multiflora*. Mature leaves are contrasting dark brown and coriaceous. The buds, however, have clearly defined calyx lobes more typical of other species in *Myrcia* sect. *Aulomyrcia*. An image of a specimen from Espírito Santo cited as this species by Sobral (2007) is not a perfect match for the type.

Selected specimen. BRAZIL. **Espírito Santo:** Santa Teresa, Nova Lombardia, Reserva Biol. Augusto Ruschi, Goipabo-açu, *Vervloet 1331* (MBML).

79. *Myrcia neoschomburgkiana* E. Lucas & C. E. Wilson, nom. nov. Replaced name: *Marlierea schomburgkiana* O. Berg, Linnaea 29: 209. 1858, non *Myrcia schomburgkiana* O. Berg, Linnaea 27: 110. 1855. TYPE: Guyana. Upper Demarara River, Sep. 1889, *G. S. Jenman 4176* (neotype, designated by McVaugh [1969: 68], K-000330632!). [Species group B].

Habitat and distribution. *Myrcia neoschomburgkiana* is found in forests and on riversides from northern South America to Peru; it occurs at altitudes of 100–1000 m.

IUCN Red List category. *Myrcia neoschomburgkiana* is known to us from 27 collections from 23 localities and is well represented in online herbaria. The EOO is estimated at > 300,000 km², including areas under low specific environmental threat. *Myrcia neoschomburgkiana* is assessed as Least Concern (LC) under IUCN criteria (2014).

Notes. McVaugh (1969) suggests resemblance of *Myrcia neoschomburgkiana* to *M. graciliflora*. This species also resembles *M. caudata* and *M. neotovarensis* in its reduced inflorescence and acuminate leaves, suggesting inclusion in the group of species defined by McVaugh (1958) as *Marlierea* sect. *Myrciopsis*. An annotation on TROPICOS® (2015) cites *Spruce 1505* as the type. We can find no reference to this or this collection, and the protologue provides no collection or locality.

Selected specimens. ECUADOR. **Morona-Santiago:** Taisha, *Cazalet* 7525 (NY). FRENCH GUIANA. **Potaro-Siparuni:** Upper Potaro River, 0–2 km N of camp, NE of toe slope of Mt. Wokomung, *Clarke* 1909 (K). GUYANA. **Cuyuni-Mazaruni:** Kamarang, trail W of airstrip, *Boom* 8311 (K). **Upper Demerara-Berbice:** Anarika, 5 mi. E of Essequibo River, *Chanderbali* 34 (K). PERU. **Loreto:** Requena, *Cheta* 161 (K). SURINAME. **Nickerie:** Kabalebo Dam Project, *Lindeman* 367 (K). VENEZUELA. **Bolívar:** Gran Sabana, 10 km SW of Karaurin Tepui, *Liesner* 23633 (K).

80. *Myrcia neosuaveolens* E. Lucas & C. E. Wilson, nom. nov. Replaced name: *Marlierea suaveolens* Cambess., Fl. Bras. Merid. 2: 374. 1833, non *Myrcia suaveolens* Cambess., Fl. Bras. Merid. 2: 315. 1833. TYPE: Brazil, 1816–1824, *A. F. C. de Saint-Hilaire s.n.* (lectotype, designated here [likely holotype], P-00217963!; isoelectotypes, MPU-010973!, P-00217963!). [Species group E].

Habitat and distribution. *Myrcia neosuaveolens* is found on the hillsides and primary forests of southeastern Brazil, from Rio de Janeiro to Santa Catarina, at altitudes of 300–1100 m.

IUCN Red List category. *Myrcia neosuaveolens* is a widespread (EOO > 230,000 km²), distinctive, and well-collected species. It is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia neosuaveolens* is a species with small elliptic-acuminate leaves and reduced inflorescences. Specimen records with qualified identifications available online without images (e.g., *A. L. Peixoto* 3283, MO not seen) suggest this species may also occur in Espírito Santo.

Selected specimens. BRAZIL. **Paraná:** Campina Grande do Sul, Sítio do Belizário, *Hatschbach* 16878 (NY). **Rio de Janeiro:** Petrópolis, Correias, Bon fim, *Marques* 129 (K). **Santa Catarina:** Braço Joaquim, Luis Alves, Itajaí, *Klein* 2055 (NY). **São Paulo:** Sete Barras, PE Carlos Botelho, *Lucas* 85 (K).

81. *Myrcia neotomentosa* E. Lucas & C. E. Wilson, nom. nov. Replaced name: *Marlierea tomentosa* Cambess., Fl. Bras. Merid. 2: 373. 1833, non *Myrcia tomentosa* (Aubl.) DC., Prodr. [de Candolle] 3: 245. 1828. TYPE: Brazil. São Paulo, 1816–1821, *A. F. C. de Saint-Hilaire s.n.* (lectotype, designated here [likely holotype], MPU-010974!; isoelectotypes, MICH-1109454!, P-01902216!, P-01902217!). [Species group E].

Myrcia strigipes Mart., Flora 24 (2 Beibl.): 108. 1841. TYPE: [Brazil.] Ad Ilheos, 1841, *C. F. P. Martius* 686 (lectotype, designated here, BR-0000005236510!; isoelectotypes, BM-000884401!, BR-0000005236428!, F-

0044416F!, F-0065397F!, G-00223165!, G-00223166!, HAL-0107497!, K-000001427!, K-000001428!, LE-00007230!, LE-00007232!, LE-00007233!, M-0171093!, M-0171094!, MICH-1109545!, NY-00405483!, P-01902218!, P-01902219!, W-0025480!, W-18890341993!).

Habitat and distribution. *Myrcia neotomentosa* is found within the moist forests of eastern Brazil, from Bahia to Santa Catarina, at altitudes of 50–1200 m.

IUCN Red List category. *Myrcia neotomentosa* is a widespread (EOO > 500,000 km²), distinctive, and well-collected species. *Myrcia neotomentosa* is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. Lectotypifications for *Marlierea tomentosa* and *Myrcia strigipes* follow annotations available online (Global Plants, 2015) made by Kazue Matsumoto during studies of southeastern Brazilian *Marlierea*, but not formally published. For the latter species, the specimen in BR represents the most complete material, so we have maintained it as the lectotype over the M holdings. *Myrcia neotomentosa* is an abundantly pubescent species of the group with thickened leaves, a raised adaxial midvein, and long, whorled, terminal inflorescences.

Selected specimens. BRAZIL. **Bahia:** Ramal a esquerda na estrada Ubaitaba/Itacaré, a 4 km do loteamento da Marambaia, *Amorim* 449 (NY). **Espírito Santo:** Praia dos Neves, ca. 3 km ao N da divisa com RJ, *Araújo* 5614 (NY). **Paraná:** Jacerehy, *Jönsson* 79 (K). **Rio de Janeiro:** Teresópolis, Serra dos Órgãos, Pedra do Sino, *Matsumoto* 712 (K). **Santa Catarina:** Brusque, Mata S. Pedro, *Klein* 135 (NY). **São Paulo:** Ubatuba, Serra do Mar, along rd. from Ubatuba to Taubate. Km. 78–89, *Morawetz* 19875 (K).

82. *Myrcia neotovarensis* E. Lucas & C. E. Wilson, nom. nov. Replaced name: *Marlierea towarensis* O. Berg, Linnaea 27: 13. 1855, non *Myrcia towarensis* O. Berg, Linnaea 27: 118. 1855. TYPE: Venezuela. Tovar, s.d., *J. W. K. Moritz* 1629 (holotype, B†; lectotype, designated here, BM-000953741!; isoelectotypes, BM-000953746!, F-0044417F!, GH-00069928!, K-000261019!, K-000330860!, NY-00405309!, P-01902213!, P-01902214!). [Species group B].

Habitat and distribution. *Myrcia neotovarensis* is found in subalpine Venezuela; its altitude is not precisely known.

IUCN Red List category. *Myrcia neotovarensis* is known only from the type (hence a very restricted EOO), from a relatively well-botanized area. The exact type locality is unspecified and not known to be

protected, but subalpine Venezuela is generally threatened by ongoing deforestation, putting local endemics at risk. *Myrcia neotovarensis* is assessed as Vulnerable (VU D2) according to IUCN criteria (2014).

Notes. *Myrcia neotovarensis* is a species with small elliptic-acuminate leaves, channeled midveins, and reduced inflorescences that resemble *M. caudata* and *M. neosuaveolens*, suggesting an affinity with *Marlierea* sect. *Myrciopsis*.

83. *Myrcia neovelutina* E. Lucas & C. E. Wilson, nom. nov. Replaced name: *Marlierea velutina* McVaugh, Fieldiana, Bot. 29: 178. 1956, non *Myrcia velutina* O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14(1): 182. 1857. TYPE: Brazil. Guapore: Falls of Madeira, Oct. 1886, *H. H. Rusby* 2683 (holotype, F-0044418F!; isotypes, G-00222985!, K-000895963!, MICH-1109451!, P-01902212!, US-00997539!). [No species group assignment].

Habitat and distribution. *Myrcia neovelutina* occurs from Peru to Brazil and has been recorded from the Madeira River and Rio Branco in Acre, Amazonas, and Rondônia; its altitude is not precisely known.

IUCN Red List category. *Myrcia neovelutina* has a wide range with few known collections, none from a known protected area. The Madeira and Rio Branco Rivers and their associated vegetation are under threat from developing hydroelectric projects in the area (EOE, 2015). *Myrcia neovelutina* is assessed as Vulnerable (VU D2) according to IUCN criteria (2014).

Notes. McVaugh (1956b) provided an unusually short description of *Myrcia neovelutina* and noted a resemblance of the indumentum to *Gomidesia*; however, the deeply tearing 4-lobed calyx prompted him to describe this species in *Marlierea*. Young fruits are ridged. In addition to the type locality, McVaugh believed the species would probably occur in Peru.

Selected specimen. BRAZIL. **Amazonas:** basin of Rio Purus, Lábrea, *Prance* 8163 (NY).

84. *Myrcia neoverticillaris* E. Lucas & C. E. Wilson, nom. nov. Replaced name: *Marlierea verticillaris* O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14: 538. 1859, non *Myrcia verticillaris* O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14(1): 206. 1857.

TYPE: Brazil. Bahia: flumen Itahype prope Castel novo, s.d., *L. Riedel* 534 (lectotype, designated here, LE-00004048!; isolectotypes, G-00222986!, K-000330440!, LE [2]!, P-00217957!). [No species group assignment].

Habitat and distribution. *Myrcia neoverticillaris* is found in the Atlantic forests and restingas of northeastern Brazil at altitudes of 10–40 m.

IUCN Red List category. *Myrcia neoverticillaris* occurs in several locations in and around Ilhéus. Although its EOO (ca. 1000 km²) is less than the minimum size for an endangered assessment, it has been collected recently and several times in the well-protected Una Biological reserve. Any change to its level of protection would result in an immediate increased threat. *Myrcia neoverticillaris* is assessed as Vulnerable (VU D2) according to IUCN criteria (2014).

Notes. *Myrcia neoverticillaris* is defined by its verticillate leaves and is clearly of the group with thickened leaves, a raised adaxial midvein, and long, densely whorled (verticillate), terminal inflorescences.

Selected specimen. BRAZIL. **Bahia:** Una, Reserva Biol. Mico-Leão, entrada no Km. 46 da Rod. BA-001 Ilhéus/Una, *Amorim* 1427 (NY).

85. *Myrcia neuwiedean* (O. Berg) E. Lucas & C. E. Wilson, comb. nov. Basionym: *Rubachia neuwiedean* O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14: 29. 1857. *Marlierea neuwiedean* (O. Berg) Nied. in H. G. A. Engler & K. A. E. Prantl, Nat. Pflanzenfam. 3(7): 77. 1893. TYPE: [Brazil.] Rio de Janeiro, s.d., *A. P. M. Neuwied* s.n. (lectotype, designated here [likely holotype], BR-0000005236541!; isolectotype, MEL not seen). [Species group E].

Habitat and distribution. *Myrcia neuwiedean* occurs in the Atlantic forests of Brazil, from Bahia to Espírito Santo, at altitudes from 5 to 70 m.

IUCN Red List category. *Myrcia neuwiedean* is a relatively well- and recently collected species with an EOO > 16,000 km² occurring only but frequently in littoral vegetation of the Atlantic forest and under acute environmental threat. Due to its relative frequency of collection as evidenced by gatherings listed on SpeciesLink (2015), *M. neuwiedean* is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia neuwiedean* is a distinctive species with cordate leaves and conspicuous bracts that subtend the flowers.

Selected specimens. BRAZIL. **Bahia:** Santa Cruz Cabralia, arredores, *Hatschbach* 53479 (NY). **Espírito Santo:** Linhares, Res. Comp. Vale do Rio Doce, estrada Gávea, Km. 4.5, *Lucas* 886 (K).

86. *Myrcia nubicola* McVaugh, Mem. New York Bot. Gard. 18: 116. 1969. TYPE: Venezuela. Amazonas: Cerro Huachamacari, Rio Cunucuma, summit camp vic., 6–17 Dec. 1960, *B. Maguire* 30045 (holotype, MICH-1109499!; isotypes, NY-00405458!, US-00117763!, VEN-76095!). [No species group assignment].

Habitat and distribution. *Myrcia nubicola* is common on steep slopes in elfin forests of southern Venezuela to Guyana at altitudes between 1000 and 2300 m.

IUCN Red List category. *Myrcia nubicola* is known to us from three collections from three localities but cited by McVaugh (1969) as one of the best-collected species of the Guyana Highlands and well represented in online herbaria. Its EOO is > ca. 150,000 km² from an area under low specific environmental threat. *Myrcia nubicola* is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia nubicola* is a short (leaves 2–5 cm), ovate-leaved species with smooth petioles and abundant axillary panicles. *Myrcia nubicola* has four calyx lobes and was described by McVaugh in *Myrcia* sect. *Aulomyrcia*. The calyx lobes are internally glabrous, the petiole is smooth, and the panicle is relatively symmetrical, making it unlikely to be of the decorticans complex of Holst and Kawasaki (2004) despite its revolute, small leaves. Holst (2002) provided additional specimen citations.

Selected specimens. GUYANA. Mt. Ayanganna, easternmost peak, Cuyuni-Mazaruni, *Pipoly* 11115 (CAY, K). VENEZUELA. **Amazonas:** *Nee* 31112 (NY). **Bolívar:** Cedeno, Meseta de Jaua, *Huber* 13036 (K).

87. *Myrcia obversa* (D. Legrand) E. Lucas & C. E. Wilson, comb. nov. Basionym: *Rubachia spathulata* O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14: 535. 1859. Replaced name: *Marlierea obversa* D. Legrand, Comun. Bot. Mus. Hist. Nat. Montevideo 3(40): 28. 1962, non *Myrcia spathulata* (O. Berg) Kiaersk., Enum. Myrt. Bras. 72. 1893. TYPE: [Brazil.]

Rio de Janeiro: ad vicum Uba, Aug. 1821, *L. Riedel* s.n. (lectotype, designated here, LE-00004049!; isoelectotypes, LE [3]!, P-05209045!). [Species group A].

Habitat and distribution. *Myrcia obversa* is known from littoral Atlantic forests of Rio de Janeiro to Bahia, Brazil, at an altitude of ca. 50 m.

IUCN Red List category. *Myrcia obversa* has an EOO of ca. 36,000 km²; it is known to us from six collections from five localities but is common in local Brazilian herbaria (speciesLink, 2015). *Myrcia obversa* is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia obversa* is a distinct species often with particularly large fruit (to 3 cm diameter). Leaves are decussate with corky petioles; the bark is thickened and shiny below the inflorescence, with the scars of previous inflorescences visible at the nodes. Thickened inflorescence rachises and petioles of young leaves are covered in straw-colored hairs. Buds are large (ca. 0.6 mm wide). Bracts often subtend buds and inflorescences. *Myrcia obversa* is related to congeners with thickened leaves, raised midveins on adaxial blades, and long, whorled, terminal inflorescences such as in *M. insularis* and *M. hexasticha*.

Selected specimens. BRAZIL. **Bahia:** Porto Seguro, Reserva Flor. Porto Seguro, CVRD, *Folli* 849 (K). **Espírito Santo:** Linhares, Reserva Ecologica de Linhares, CVRD, Estrada Jacaranda, *Matsumoto* 820 (K).

88. *Myrcia platyclada* DC., Prodr. [de Candolle] 3: 244. 1828. TYPE: French Guiana, s.d., *Anonymous* s.n. (holotype, G-DC not seen, G-DC photo at F!). [Species group C].

Habitat and distribution. *Myrcia platyclada* has been collected from lowland tropical rainforest, from the Lesser Antilles and Panama to northern Brazil, from altitudes of ca. 300–700 m.

IUCN Red List category. *Myrcia platyclada* is an extremely widespread species and is considered of Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia platyclada* has symmetrical architecture, absent bracts, discoloured leaves, and faint blade venation; it is reminiscent of *M. exploratoris* from which it differs in its glabrous flowers and axes. *Myrcia exploratoris* grows at consistently higher altitudes. The leaves of *M. platyclada* are distinctly

spatulate but can have blunt-acuminate to rounded tips. Santos (2014) recorded *M. platyclada* as emerging in a clade that corresponds to species group C as presented here. Holst (2002) provided additional specimen citations.

Selected specimens. BRAZIL. **Amapá:** Mazagão Camai-pi, EMBRAPA Reserve & vic., 30 km NW of Mazagão, *Mori* 17514 (K). **Amazonas:** Presidente Figueiredo, próximo ao igarapé, *Santos* 766 (K). **Pará:** Rod. Belém–Brasília, Km. 97, *Kulhmann* 176 (K). **Roraima:** Mt. Roraima, *E Ule* 8672 (K). FRENCH GUIANA. **Cayenne:** Fleuve Sinnamary, env. 3400 km sur la river Courcibo, *Oldeman* 1182 (K). GRENADA. s. loc., *Sherring* s.n. (K). GUYANA. **Cuyuni-Mazaruni:** Pakaraima Mtns., *Hoffman* 1746 (K). ST. LUCIA. Fond St. Jacques, *Ramage* s.n. (K). SURINAME. **Sipaliwini:** Lely Mtns., SW plateau, *Lindeman* 251 (K). TRINIDAD AND TOBAGO. Arima Blanchisseuse, *Marshall* 12680 (K).

89. *Myrcia polyantha* DC., Prodr. [de Candolle] 3: 252. 1828. TYPE: Brazil. Bahia: in campestribus apricis supra granitiden, prope S. Anna in desertis, s.d., *C. F. P. Martius* s.n. (lectotype, designated here, M-0136912!; isolectotypes, K-000262364!, M-0136911!). [Species group C].

Habitat and distribution. *Myrcia polyantha* is found in northeastern Brazil, from Piauí to Bahia and Goiás in tabuleiro, cerrado, and scrubby forest vegetation and on sandy soils at altitudes of 50–500 m.

IUCN Red List category. *Myrcia polyantha* is known to us only from the type and one other collection. Approximately 60 authoritatively named specimens are cited online (speciesLink, 2015), indicating a relatively common species with an EOO > 20,000 km². *Myrcia polyantha* is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. The type of *Myrcia polyantha* has tightly bunched whorls of inflorescences emerging at a single bracteose node, a characteristic more usually associated with species emerging in clade 8 of Lucas et al. (2011) such as *M. tomentosa*. However, the venation and bud shape of this species are reminiscent of *M. multiflora* as are specimens with images available on Lista do Brasil (Sobral et al., 2015); on balance, this persuades us to include the species in *Myrcia* sect. *Aulomyrcia*; it also emerges in this group in the study of Staggemeier et al. (2015). No material of the Martius type collection was found in the BR herbarium.

Selected specimen. BRAZIL. **Bahia:** Subaúma, Entre Rios, 1 Jan. 1997, *Sobral* s.n. (FURB).

90. *Myrcia porphyrea* McVaugh, Mem. New York Bot. Gard. 18: 119. 1969. TYPE: British Guiana [Guyana.] Pakaraima Mtns., Imbaimadai savannas, upper Mazaruni River, 21 Oct. 1951, *B. Maguire* 32159 (holotype, MICH-1109562!; isotypes, NY-00405467!, US-00117769!, VEN-76154!). [Species group C].

Habitat and distribution. *Myrcia porphyrea* is endemic to the Imbaimadai region of the Pakaraima Mountains in Cuyuni-Mazaruni, Guyana, with an altitude of ca. 550 m.

IUCN Red List category. *Myrcia porphyrea* is known to us from five gatherings, each close to the type locality. *Myrcia porphyrea* has a very restricted EOO in an area we assume to be unprotected and under threat from mining activity (EOE, 2015). *Myrcia porphyrea* is assessed as Vulnerable (VU D2) according to IUCN criteria (2014).

Notes. *Myrcia porphyrea* is very distinct in its thick reticulate leaves. Inflorescences, particularly in bud, are similar to those of *M. inaequiloba* in having short pedicels, small buds that dry darkly colored (vs. the pale or reddish hairs that cover the inflorescence axes), and outer calyx lobes. McVaugh (1969) struggled to assign this species to a section.

Selected specimen. GUYANA. Cuyuni-Mazaruni, Imbaimadai, Upper Mazaruni River, *Davis* 348 (K).

91. *Myrcia portoricensis* (Britton) Cedeño-Mald. & Breckon ex F. S. Axelrod, Syst. Vademec. Vasc. Pl. Puerto Rico, 227. 2011. Basionym: *Calyptranthes portoricensis* Britton, Bull. Torrey Bot. Club 51: 11. 1924. TYPE: Puerto Rico. Monte Alegrillo, 1 Jan. 1913, *F. L. Stevens* 4718 (holotype, NY00084464!). [Species group B].

Habitat and distribution. *Myrcia portoricensis* is endemic to the montane forests of Puerto Rico at altitudes of ca. 300–800 m.

IUCN Red List category. *Myrcia portoricensis* is known to us from five collections including those of the synonymous *M. portoricensis* Alain, all from the Maricao forest. The Maricao State Forest Reserve is under relatively low environmental pressure; therefore, this species should be under low threat, despite its apparently very restricted distribution and low population size. This species is of Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia portoricensis* is remarkable in its extremely regular, terminal cymose inflorescences that are reminiscent of strictly cymose species from *Calyptranthes* or clade 7 of Lucas et al. (2011) in addition to calyptrate flowers. Santos (2014) found the species to emerge in the clade of *Myrcia* sect. *Aulomyrcia*, which made it possible to see associated characters, such as flattened rachises and cymose inflorescences, as found in species group B.

Selected specimen. PUERTO RICO. Maricao state forest, Rd. 120, Km. 15.6 (S side), *Proctor 41752* (IJ).

92. *Myrcia ptariensis* (Steerm.) McVaugh, Mem. New York Bot. Gard. 18: 103. 1969. Basionym: *Aulomyrcia ptariensis* Steerm., Fieldiana, Bot. 28: 1006. 1957. TYPE: [Venezuela.] Bolívar: Ptari-tepui, 1 Nov. 1944, *J. A. Steyermark 59724* (holotype, F-0064758F!; isotype, U-0005137!). [No species group assignment].

Habitat and distribution. *Myrcia ptariensis* is known from forested sandstone on the tepuis of Venezuela in Bolívar from altitudes of ca. 1700–1800 m.

IUCN Red List category. *Myrcia ptariensis* is known to us from eight relatively close collections, with an EOO < 2000 km². Apparently locally common on the tepuis of Bolívar State in Venezuela, the species is not well represented; this is likely due to low levels of collecting in the area. The tepuis of Venezuela are subject to significant local threats (EOE, 2015), but their inaccessibility means that their vegetation is mostly intact. *Myrcia ptariensis* is assessed as Vulnerable (VU) according to IUCN criteria (2014).

Notes. Steyermark believed *Myrcia ptariensis* has an affinity to *M. neobuxifolia*. *Myrcia ptariensis* is distinguished by reduced hairy inflorescences, smooth petioles, and a raised midvein on adaxial blade surfaces.

Selected specimen. VENEZUELA. Bolívar: Auyan-tepui, Ro Lomita camp, *Steyermark 93596* (K).

93. *Myrcia pubiflora* DC., Prodr. [de Candolle] 3: 249. 1828. *Aulomyrcia pubiflora* (DC.) O. Berg, Linnaea 27: 40. 1855. TYPE: Brazil. [Minas Gerais:] Minarum, Serro Frio, s.d., *C. F. P. Martius s.n.* (lectotype, designated here [likely holotype], M-0136896!; isolectotypes, G-DC!, P [3!]). [Species group C].

Aulomyrcia pohliana O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14: 72. 1857. TYPE:

[Brazil.] Minas Gerais, s.d., *J. B. E. Pohl 1080* (holotype, B†; lectotype, designated here, W-0037132!; isolectotypes, F-0064755F!, K-000342674!, K-000342675!, W-0037133!).

Habitat and distribution. *Myrcia pubiflora* is distributed along the length of the Brazilian Atlantic Rainforest from Sergipe to Santa Catarina at altitudes of ca. 10–1500 m.

IUCN Red List category. *Myrcia pubiflora* is known to us from seven collections from Minas Gerais, Rio de Janeiro, and Santa Catarina in Brazil; it is, however, well represented in local herbaria available online (speciesLink, 2015). The EOO of this species is large enough to remove it from a category of threat; therefore, it is considered Least Concern (LC) according to IUCN criteria (2014).

Notes. The lectotype of *Aulomyrcia pohliana* at W bears the number 3058 in addition to the collection number and the serial number 31530 from the US negative set.

Selected specimens. BRAZIL. **Espírito Santo:** Linhares, Reserva Natural Vale do Rio Doce, proximo a estrada 154, talhão 506, *Lino 82* (K). **Minas Gerais:** Ouro Preto, Camarinhas, *Peron 685* (K). **Rio de Janeiro:** *Glaziou 10842* (K, US). **Santa Catarina:** Sanga da Areia, Sombrio, *Reitz 9657* (NY).

94. *Myrcia pudica* (McVaugh) E. Lucas & C. E. Wilson, comb. nov. Basionym: *Marlierea pudica* McVaugh, Brittonia 33: 35. 1981. TYPE: Venezuela. Bolívar: Cerro Guaiquinima, secto NO, entre los brazos NO del Rio Carapo, 30 May 1978, *J. A. Steyermark 117522* (holotype, MICH-1109598!; isotypes, F-0065393F!, VEN-128765!). [Species group B].

Habitat and distribution. *Myrcia pudica* was collected from stony, sandy plateau vegetation in Venezuela at an altitude of ca. 1000 m.

IUCN Red List category. *Myrcia pudica* is known to us only from the type available online and the one specimen cited below, which is collected from the same, unprotected vicinity. The Venezuelan tepuis have not been exhaustively botanized, but the Myrtaceae of the Guiana shield is relatively well known (McVaugh, 1958, 1969), leading us to believe this species may have a very restricted EOO (less than five locations). *Myrcia pudica* is assessed as Vulnerable (VU D2) according to IUCN criteria (2014).

Notes. *Myrcia pudica* is an extremely distinctive species with elliptic, straplike leaves, three or four calyx lobes, and two locules or “imperfectly three” (Steyermark, 1981). The reduced inflorescence suggests an affinity with McVaugh’s (1958) *Marlierea* sect. *Myrciopsis*.

Selected specimen. VENEZUELA. **Bolívar:** Heres, Meseta del Guaiquinima, Rio Carapo 8 km N del Salto Carapo, Huber 12399 (K, US).

95. *Myrcia pyrifolia* (Desv. ex Ham.) Nied., Nat. Pflanzenfam. 3(7): 76. 1893. Basionym: *Eugenia pyrifolia* Desv. ex Ham., Prodr. Pl. Ind. Occid., 44. 1825. *Aulomyrcia pyrifolia* (Desv. ex Ham.) O. Berg, Linnaea 27: 44. 1855. TYPE: Guyana, s.d., herb. Prof. Desv. s.n. (holotype, P-00725813!). [Species group D].

Aulomyrcia pyrifolia (Desv. ex Ham.) O. Berg var. *robusta* O. Berg, Linnaea 27: 44–45. 1854 [1855]. TYPE: [French Guiana.] Guiana Gallica. s.d., P. A. Poiteau s.n. (holotype, B†; lectotype, designated here, LE!).

Habitat and distribution. *Myrcia pyrifolia* is known from moist riverine forests of Venezuela, Guyana, Suriname, French Guiana, and Brazil at altitudes of ca. 300–600 m.

IUCN Red List category. *Myrcia pyrifolia* is a well-collected species known to us from 23 collections and 19 localities, with an EOO of ca. 550,000 km². *Myrcia pyrifolia* is considered of Least Concern (LC) according to IUCN criteria (2014).

Notes. The type collection of *Myrcia pyrifolia* has a strong resemblance to *M. amazonica* but with a convex to flat midvein on the adaxial blade surface. The outside of the ovary is densely white-pubescent and leaves are acuminate, which are characters that also differentiate *M. pyrifolia* from *M. amazonica*. McVaugh (1969) suggested affinities to *M. rufipila* and related species that are distinguished by internally pubescent calyx lobes. The calyx lobes in *M. pyrifolia* are internally glabrous as are those in *M. amazonica*. The lectotype of *Aulomyrcia pyrifolia* var. α *robusta* was not seen by McVaugh (1969) but has an impressed midvein, as does *M. amazonica* but not *M. pyrifolia*. For these reasons the varietal status of *M. pyrifolia* var. *robusta* should be tested. Berg (1855–1856) indicated “v. in hb. Kunth” for the type collection of the latter variety; the Kunth herbarium was subsumed into the herbarium at Berlin before the destruction of the latter.

Selected specimens. BRAZIL. **Pará:** Oriximiná, Igarapé Jaramacaru, campos de Ariramba, Martinelli 12268 (K, US). FRENCH GUIANA. Montagne du Mahury, Ile de

Cayenne, Descoings 20114 (CAY). GUYANA. Upper Canje River, betw. Digitima savanna, E Berbice-Corentyne, Gillespie 2587 (CAY). SURINAME. **Marowijne:** via secte ab Moengo tapoe ad Grote Zwiebelzwamp, Lanjouw 559 (K). **Sipaliwini:** Nassau, forest near Km. 8.2, Lanjouw 2666 (K).

96. *Myrcia quitarensis* (Benth.) Sagot, Ann. Sci. Nat., Bot., VI, 20: 184. 1885. Basionym: *Eugenia quitarensis* Benth., J. Bot. (Hooker) 2: 322. 1840. *Myrciaria quitarensis* (Benth.) O. Berg, Linnaea 27: 323. 1856. TYPE: [British Guiana.] Banks of the Rio Quitaro, 1838, R. Schomburgk 547 (lectotype, designated here [likely holotype], K000344106!; isoelectotypes, E-00394769!, F-0065291F!, F-0065292F!, F-0065293F!, G-00223836!, K-000344107!, L-0329642!, P-00163116!, P-00725816!, US-00048585!, W-0037141!). [Species group C].

Habitat and distribution. *Myrcia quitarensis* has been collected from riverbanks of southeastern Venezuela to Guyana (possibly also French Guiana), from an altitude not precisely known.

IUCN Red List category. The collection Larpin 632 (CAY not seen) records *Myrcia quitarensis* from French Guiana, extending its known distribution. Based on all available information, this species has a large EOO but a highly fragmented distribution, and it is rarely reported from otherwise well-collected areas. *Myrcia quitarensis* is assessed with possible status of Near Threatened (NT) according to IUCN criteria (2014).

Notes. *Myrcia quitarensis* has four calyx lobes and a convex to flat midvein on the adaxial leaf blade. The lectotypification process began in 1969 when McVaugh annotated the K sheet from Bentham’s herbarium as type and the remaining K sheet as isotype. McVaugh (1969) reported a resemblance of *M. quitarensis* to *M. pyrifolia* in his *Myrcia* sect. *Aulomyrcia* but assigns *M. quitarensis* to *Myrcia* sect. *Armeriela* as the hypanthium tears deeply at anthesis. Holst (2002) described a species with two pairs of unequal calyx lobes, a convex midvein, nearly glabrous flowers, and reddish, dibrachiate inflorescence trichomes; additional specimen citations are also provided.

Selected specimen. GUYANA. **Potaro-Siparuni:** Iwokrama Rainforest Reserve, Clarke 692 (U).

97. *Myrcia racemosa* (O. Berg) Kiaersk., Enum. Myrt. Bras. 72. 1893. Basionym: *Aulomyrcia racemosa* O. Berg, Linnaea 27: 52. 1855. TYPE: [Brazil.] Rio de Janeiro: Ilha de Governador, s.d., C. F. P. Martius 36 (lectotype, designated

here [likely holotype], BR-0000005280674!; isoelectotypes, K-000344110!, LE!). [Species group C].

Habitat and distribution. *Myrcia racemosa* is widespread, distinct, and well collected in the Brazilian Atlantic forests, and is found from southeastern Bahia to northern Santa Catarina, at altitudes of ca. 10–1600 m.

IUCN Red List category. Material of *Myrcia racemosa* available to us represents 69 collections from 48 localities with an EOO > 3 million km². *Myrcia racemosa* is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. Berg's two syntypes of *Myrcia racemosa* present variable morphology. We take that with pubescent fruits and more open venation represented by *Martius 36* as the more common form and lectotypify this collection, as opposed to *J. B. E. Pohl 1091* (as Schott, W!). Future studies may delimit one or more species from within this interpretation of *M. racemosa*. In the sense considered here, *M. racemosa* is a distinctive species with coriaceous, open-veined leaves, and usually pubescent branchlets, petioles, and peduncles. An affinity with *M. micropetala* is suggested by the DNA-based study of Lucas et al. (2011); there is similarity in their impressed, looping venation and bristly gray or straw-colored hairs.

Selected specimens. BRAZIL. **Bahia:** Una, Estrada que liga São José com Una, a 17 km da BR 101, ca. de 45 km ao S de Itabuna, *Mori 11895* (K). **Espírito Santo:** Estr. Rod. do Sol, 10 km depois de Guarapari, *de Lima 2933* (K). **Minas Gerais:** Serra de Ibitipoca, *Sucre 7378* (K). **Paraná:** Morretes, Est. Marumbi, *Hatschbach 25367* (K, NY); Rio São Joãozinho, *Hatschbach 40166* (NY). **Rio de Janeiro:** Restinga de Tijuca, *Sucre 8042* (K). **Rondônia:** eixo da JP-14, ponto II, *Toledo 201* (ESA). **Santa Catarina:** Mina Velha, Garuva, São Francisco do Sul, *Reitz 4633* (US). **São Paulo:** Peropava, Faz. Boa Vista, *Catharino 359* (ESA); Loteamento Maramba II, 6 km de Itanhaém em direção a Peruíbe, *Romão 705* (ESA). **Sergipe:** Santa Luzia do Itanhi, ca. 2.5 km do Distr. Crasto, na estrada para Sta. Luzia do Itanhi, *Amorim 1466* (NY).

98. *Myrcia racemulosa* DC., Prodr. [de Candolle] 3: 254. 1828. TYPE: [Brazil.] prov. Minarum, s.d., *C. F. P. Martius s.n.* (lectotype, designated here [likely holotype], M-0136833!; isoelectotypes, G-DC!, M-0136832!, M-0136834!, M-0136835!). [Species group C].

Myrcia imbricata Gardner in H. B. Fielding & G. Gardner, Sert. Pl., t. 75. 1844. TYPE: Brazil. Minas Gerais: Serra dos Araras, confines of Goyaz, s.d., *G. Gardner 4646* (lectotype, designated here [likely holotype],

BM-0953613!; isoelectotypes, K-000343387!, K-000343388!).

Myrcia scutulifera DC., Prodr. [de Candolle] 3: 254. 1828. TYPE: [Brazil.] prov. Minarum, s.d., *C. F. P. Martius s.n.* (lectotype, designated here [likely holotype], M-0136832!; isoelectotype, G-DC!).

Habitat and distribution. *Myrcia racemulosa* is a species of the Central Brazilian cerrado and campo rupestre found from Bahia to Mato Grosso do Sul at altitudes of 500–1000 m.

IUCN Red List category. *Myrcia racemulosa* is an infrequent species known to us from the types and two further collections. Approximately 20 reliably named specimens available online (SpeciesLink, 2015) give an EOO > 500,000 km². *Myrcia racemulosa* is assessed as Least Concern (LC) according to IUCN criteria (2014), although its relative rarity may mean a detailed assessment would result in a higher category of threat.

Notes. *Myrcia racemulosa* has affinities with *M. myrtillofolia* but is distinct in its sessile, cordate leaves that clasp the stem and its consistently acute leaf tips. Individuals are usually lightly pubescent in contrast to *M. myrtillofolia*, which is mostly glabrous.

Selected specimens. BRAZIL. **Bahia:** Barreiras, Rodovia Barreiras–Brasília Km. 90, *Coradin 7417* (K). **Goiás:** Caldas Novas, *Vieira 1627* (K). **Minas Gerais:** Chapada dos Gaúchos, *da Silva 109* (K).

99. *Myrcia ramuliflora* (O. Berg) N. Silveira, Roesslária 7: 66. 1985. Basionym: *Aulomyrcia ramuliflora* O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14: 64. 1857. TYPE: [Brazil.] Bahia, s.d., *P. Salzmann s.n.* (holotype, B†; neotype, designated here, Brazil, Bahia, Salvador, Lagoa de abaeté, Salvador, 22 May 1981, *S. A. Mori 14039*, CEPEC 27425!; isoneotypes, MO-1709009!, NY-1522713!, RB-00264855!). [Species group C].

Myrcia sphenoides (O. Berg) Mattos, Lofgrenia 126: 3. 2008. Basionym: *Aulomyrcia sphenoides* O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14: 63. 1857. TYPE: [Brazil.] Bahia: ad Soteropolin prov. Bahia, s.d., *Blanchet 1825* (holotype, B†; lectotype, designated here, G-00222042!; isoelectotypes, BM-2!, BR-0000005238309, HAL-0089718!, P-05262132!).

Habitat and distribution. *Myrcia ramuliflora* is endemic to the restingas of Bahia at altitudes of 0–60 m.

IUCN Red List category. Approximately 40 authoritatively named specimens are available online (speciesLink, 2015) providing an EOO > 15,000

km². *Myrcia ramuliflora* is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. Material cited of *Myrcia ramuliflora* on-line from Sergipe and Rio Grande do Norte are morphologically very different and likely of a separate taxon. *Myrcia ramuliflora* resembles *M. littoralis* but differs in the relative absence of trichomes (sparse trichomes on new branches only) and in having venation raised on both sides of the leaves. The need for a neotype arises from the destruction of the only apparent specimen of the Salzmann gathering. The neotype was selected as it is a good match for the protologue, was collected from a similar locality, and is widely available in disparate herbaria.

Selected specimens. BRAZIL. **Bahia:** Mata de São João, Praia do Forte, na beira da avenida de entrada, *Lima 412* (K); entre Rios, sudoeste do povoado de Subaúma, *França 1142* (HUEFS).

100. *Myrcia revolutifolia* McVaugh, Mem. New York Bot. Gard. 18: 121. 1969. TYPE: Venezuela. Amazonas: Serrania Yutaje, Rio Manapiare, Cerro Coro-Coro, 2 Mar. 1953, *B. Maguire 35462* (holotype, MICH-1109559!; isotypes, F-0065558F!, NY-00405472!, US-00117771!, VEN-75664!). [No species group assignment].

Habitat and distribution. *Myrcia revolutifolia* is known from sandy savanna and forest patches of southeastern Colombia to northern Brazil from altitudes between 600 and 2300 m.

IUCN Red List category. Collections of *Myrcia revolutifolia* available to us indicate that the species has an EOO of ca. 40,000 km² and has been frequently collected. *Myrcia revolutifolia* is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia revolutifolia* is a shrub or small tree distinguished by five free, internally pubescent calyx lobes, revolute leaves, terminal bunches of asymmetrical, glabrous inflorescences with dark red, smooth branchlets and petioles, and by pale gray, lightly decorticating bark. Holst (2002) provided a detailed discussion and many additional specimen citations.

Selected specimens. VENEZUELA. **Amazonas:** Serrania Paru, SW sector, *Berry 4933* (K). **Bolívar:** Meseta del Jaua, Cerro Sarisarinama, *Steyermark 109176* (K).

101. *Myrcia riodocensis* G. M. Barroso & Peixoto, Acta Bot. Brazil. 4(2): 13. 1990. TYPE: [Brazil.] Espírito Santo: Linhares, 30 Jan. 1972, *D. Sucre*

8269 (lectotype, designated here, RB-00542159!; isoelectotypes, CVRD!, MBML not seen, RB-00662387!). [Species group D].

Habitat and distribution. *Myrcia riodocensis* is known from the high Atlantic rainforest of eastern Brazil in Espírito Santo at an altitude of ca. 30 m.

IUCN Red List category. *Myrcia riodocensis* was assessed as Critically Endangered (CR) by Martinelli and Moraes (2013) according to IUCN criteria (2014).

Notes. The protologue affiliates *Myrcia riodocensis* with *Myrcia* sect. *Aulomyrcia*, and we take this to mean sensu Grisebach (1864). The type specimen has a channeled midvein on the adaxial leaf blade and a pyramidal inflorescence with asymmetrical branching. Bracts are absent; the plant appears glabrous and has peeling bark. These are characters that we associate with *M. amazonica*. *Myrcia riodocensis* differs, however, in its distinctive, 4-lobed calyx and reduced inflorescence.

Selected specimen. BRAZIL. **Espírito Santo:** Linhares, Reserva Nat. CVRD, Estrada Aceiro de Viveiro, *Folli 3197* (K).

102. *Myrcia rotundata* (Amshoff) McVaugh, Mem. New York Bot. Gard. 18: 122. 1969. Basionym: *Aulomyrcia rotundata* Amshoff, Recueil Trav. Bot. Néerl. 42: 8. 1950. TYPE: British Guiana [Guyana.] Kaieteur savanna, 4 Sep. 1937, *C. I. Sandwith 1348* (holotype, MICH-1109558!; isotypes, K-000344205!, NY-00386683!, U-0061928!, US-00005294!). [Species group B].

Habitat and distribution. *Myrcia rotundata* has been collected from the Guyana shield savanna on rocky ground in Venezuela to Guyana from an altitude of ca. 366 m.

IUCN Red List category. *Myrcia rotundata* is known to us from three collections from three distinct localities. Given these, plus the material studied by McVaugh (1969), this suggests an EOO of at least 45,000 km². To our knowledge, *M. rotundata* has not been collected since Steyermark's 1964 expedition, suggesting a possible subsequent decline; therefore, it is assessed as Vulnerable (VU) according to IUCN criteria (2014).

Notes. *Myrcia rotundata* is a tetramerous species with two locules per ovule that resemble those of other small, round-leaved, montane species in *Myrcia* sect. *Aulomyrcia*. Amshoff (1950) suggested an

affinity of this species with others here grouped as species group B. Santos (2014) found a sample of *M. rotundata* to emerge outside the *Myrcia* sect. *Aulomyrcia* clade; however, this accession does not match the type collection.

Selected specimens. GUYANA. **Cuyuni-Mazaruni:** *Pipoly* 7719 (K). VENEZUELA. **Bolívar:** Oso Woods Camp, Rio Churun. Auyan-tepui, *Steyermark* 93197 (K).

103. *Myrcia rubiginosa* Cambess., Fl. Bras. Merid. 2: 300. 1832. TYPE: Brazil. Rio de Janeiro, 1816–1821, A. F. C. Saint-Hilaire s.n. (lectotype, designated here [likely holotype], P-00161371!; isoelectotypes, MPU-010964!, P-00161369!, P-00161370!). [Species group D].

Myrcia pyramidata O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14: 193. 1857. TYPE: [Brazil.] Rio de Janeiro, s.d., F. Sellow s.n. (holotype, B†; lectotype, designated here, K-000262404!; isoelectotypes, BR-0000005238545!, P-00161139!, W-0037074!).

Habitat and distribution. *Myrcia rubiginosa* was collected from the Atlantic forest of Rio de Janeiro, Brazil; its altitude is not precisely known.

IUCN Red List category. *Myrcia rubiginosa* is known to us from three 19th century collections in addition to the type. All collections were from unspecified forests in Rio de Janeiro under extreme threat. This species is assessed as Vulnerable (VU D2) according to IUCN criteria (2014). *Myrcia rubiginosa* is morphologically similar to *M. amazonica*, and, if conspecific, the EOO would be large enough to obviate environmental threat. Further study is required.

Selected specimen. BRAZIL. **Rio de Janeiro:** *Miers* 4435 (K).

104. *Myrcia rufipila* McVaugh, Mem. New York Bot. Gard. 18: 104. 1969. Replaced name: *Aulomyrcia divaricata* O. Berg, Linnaea 27: 58. 1855, non *Myrcia divaricata* (O. Berg) Lemée in Fl. Guyane Franç. 3: 146. 1954, nom. illeg. TYPE: Suriname. Upper Suriname River, Oct. 1844, A. Kappler 1702 (lectotype, designated here, W-0033247!; isoelectotypes, G-00222573!, G-00222574!, JE-00000830!, LE-00007059!, MICH-1109835!, MO-313556!, P-00551593!, P-00551594!, P-00551595!, U-0102923!, W-0037123!). [Species group C].

Habitat and distribution. *Myrcia rufipila* is known from river and coastal regions and moist

lowland forests of Amazonian Brazil, Guyana, and Suriname, from altitudes of ca. 70–300 m.

IUCN Red List category. *Myrcia rufipila* is known to us from 10 collections from eight localities; this species is unexpectedly widespread relative to the number of collections, with an EOO of ca. 900,000 km². *Myrcia rufipila* is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. McVaugh (1969) treated *Myrcia rufipila* in *Myrcia* sect. *Armeriela* and suggested an affinity to other species with internally pubescent calyx lobes and impressed midveins such as *M. subobliqua*. McVaugh (1969) also suggested an affinity to *M. pyrifolia*, but that species has internally glabrous calyx lobes.

Selected specimens. BRAZIL. **Amapá:** Serra do Navio, next to village in area prepared for mining, *Rabelo* 3156 (K, US). **Amazonas:** Reserva Flor. Adolfo Ducke, Manaus–Itacoatiara, Km. 26, *Souza* 412 (K). **Pará:** Fordlândia, Tapajós River Region, *Krukoff* 1041 (K); Ilha do Algodoal, Rochina, *Bastos* 1377 (K). **Roraima:** Boa Vista, foothills of Serra Tepequém, near Igarapé Paparu, *Prance* 4367 (K, US). GUYANA. Cuyuni-Mazaruni, Mazaruni Station, *Forest Department of British Guiana* 672 (K).

105. *Myrcia rugosior* (McVaugh) E. Lucas & C. E. Wilson, comb. nov. Basionym: *Marlierea rugosior* McVaugh, Mem. New York Bot. Gard. 18: 67. 1969. TYPE: Venezuela. Bolívar: Auyan-tepui near summit of central part of NW arm, 7 May 1964, J. A. Steyermark 93545 (holotype, MICH-1109597!; isotype, VEN-72165!). [Species group E].

Habitat and distribution. *Myrcia rugosior* was collected near the summit of the central part of the northwest arm of the Auyan tepui, in *Bonnetia* Mart. (Clusiaceae) forest, in Venezuela (Bolívar), at an altitude of ca. 1800 m.

IUCN Red List category. *Myrcia rugosior* is known to us only from the type and one other collection, *Holst* 3820 (MO not seen), which was collected from the same altitude in Bolívar. We find no evidence of environmental protection in this area. While the Venezuelan tepuis have not been vigorously botanized, the Myrtaceae of the Guiana shield are relatively well known (McVaugh, 1958, 1969), leading us to believe that *M. rugosior* may have a very restricted distribution, with known locations five or fewer. The species is assessed as Vulnerable (VU D2) according to IUCN criteria (2014).

Notes. *Myrcia rugosior* has been described as a tree to 5 m. Based on the limited material available, this species appears to fit the characteristics of *Rubachia* (sensu Berg), with an almost completely fused calyx tearing deeply to the summit of the ovary. Holst (2002) mentions *M. rugosior* in the context of *M. bonnetiasylvestris* (Steysm.) Steysm. and *M. sipapensis* McVaugh, species not included in *Myrcia* sect. *Aulomyrcia*.

106. *Myrcia rupta* M. L. Kavas. & B. Holst, Brittonia 46: 141. 1994. TYPE: French Guiana. Saul: Crique Kapiri, bassin de l'Approuague, 14 Jan. 1991, G. Cremers 11606 (holotype, U-0005148!; isotypes, ASU-0019294!, CAY!, MO-313555!, NY-00074077!, P not seen, US-00660061!). [Species group C].

Habitat and distribution. *Myrcia rupta* is an understory species from the low-altitude moist forest of French Guiana at altitudes of ca. 40–550 m.

IUCN Red List category. *Myrcia rupta* is endemic to central French Guiana but common within its range. *Myrcia rupta* is known to us from 30 collections from 15 localities and has an EOO > 165,000 km². The species is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia rupta* has asymmetrical panicles reduced to appear almost racemose, many persistent pointed bracts, a looping intramarginal vein, and a channeled midvein. Kawasaki and Holst (1994) give a clear account of their decorticans complex in the protologue of this species and justify their description of a species with a tearing calyx in *Myrcia*.

Selected specimen. FRENCH GUIANA. Saul, Vers la Crique Limonade, de Granville 2346 (K).

107. *Myrcia salticola* (Steysm.) McVaugh, Mem. New York Bot. Gard. 18: 123. 1969. Basionym: *Aulomyrcia salticola* Steysm., Fieldiana, Bot. 28: 1007. 1957. TYPE: [Venezuela.] Bolívar: Salto Iwaracaru-meru, Sororopan-tepui, 15 Nov. 1944, J. A. Steysmark 60213 (holotype, F-0064766F!; isotypes, NY-00386684!, U-0005149!, US-00048591!, VEN-37427!). [Species group D].

Habitat and distribution. *Myrcia salticola* is endemic to the waterfalls of the Sororopan-tepui of Venezuela (Bolívar); it is found at an altitude of ca. 1600 m.

IUCN Red List category. *Myrcia salticola* is known only from the type collection from a relatively poorly known and collected area; we find no evidence of environmental protection. This species appears to have an extremely restricted EOO. There are few direct threats to the higher-altitude vegetation of the Tepuis; however, fire is a source of stochastic threat to endemic species (EOE, 2015). *Myrcia salticola* is assessed as Vulnerable (VU D2) according to IUCN criteria (2014).

Notes. The protologue of *Myrcia salticola* reports resemblance to *M. tomentosa*, and there is some similarity of leaf shape and texture. However, fruiting calyces in the type material are not star-shaped or reflexed as in the species of, and those related to, *M. tomentosa*. With a slightly raised midvein and hairy pyramidal panicle, this species resembles those hypothesized to have an affinity with *M. amazonica*.

108. *Myrcia santateresana* Sobral, Novon 20: 340. 2010. TYPE: Brazil. Espírito Santo: Santa Teresa, São Lourenço, Reserva Biol. São Lourenço, trilha do Caravagem, 3 Feb. 1999, L. Kollmann 1793 (holotype, MBML!; isotype, BHCB). [Species group D].

Habitat and distribution. *Myrcia santateresana* is endemic to the higher-altitude forests of Espírito Santo, Santa Teresa, at altitudes of ca. 750–850 m.

IUCN Red List category. *Myrcia santateresana* is calculated in the protologue as being Endangered (EN) according to IUCN criteria (2014).

Notes. The protologue of *Myrcia santateresana* states affinities with *M. badia*, differentiating *M. santateresana* in having smaller leaves, differing venation, smaller flowers, and no calyx tube. *Myrcia santateresana* has paired, decussate, long, loose, terminal inflorescences. The species has five calyx lobes and a channeled midvein; the discoloured, paler venation on otherwise dark brown drying leaves is reminiscent of *M. pyrifolia*.

109. *Myrcia saxatilis* (Amshoff) McVaugh, Mem. New York Bot. Gard. 18: 105. 1969. Basionym: *Aulomyrcia saxatilis* Amshoff, Recueil Trav. Bot. Néerl. 39: 154. 1942. TYPE: Suriname. Lucie River, 14 May 1926, G. Stahel 7048 (holotype, U-0132341!; isotype, MO-313552!). [Species group C].

Habitat and distribution. *Myrcia saxatilis* is recorded from rocky soils of higher-altitude savannas

and associated forests of Brazil (Amazonas), French Guiana, and Suriname at altitudes of ca. 50–1200 m.

IUCN Red List category. *Myrcia saxatilis* is known to us from fewer than 40 collections from 26 localities and has an EOO > 280,000 km². *Myrcia saxatilis* is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia saxatilis* is a widespread and well-collected species that resembles *M. inaequiloba* but differs in having smaller, rounder leaves and corky petioles.

Selected specimens. BRAZIL. **Amazonas:** Barcelos, base of Serra Araca, 0–3 km S of Central Massif, 3 km E of Rio Jauari, *Prance 28889* (K). FRENCH GUIANA. Montagne des Nouragues, bassin de l'Approuague, *Larpin 509* (CAY). SURINAME. **Sipalwini:** Blanche Marie Waterfall on Nickerie River, *Evans 2489* (K).

110. *Myrcia scytophylla* (Diels) E. Lucas & C. E. Wilson, comb. nov. Basionym: *Marlierea scytophylla* Diels, Verh. Bot. Vereins Prov. Brandenburg 48: 187. 1906 [1907]. TYPE: [Brazil.] Amazonas: Rio Negro, São Joaquim, Jan. 1902, *E. H. G. Ule 6044* (holotype, B†; lectotype, designated here, G-00222983!; isoelectotype, F-0044415F!). [Species group C].

Habitat and distribution. *Myrcia scytophylla* is known from southern Venezuela, Brazil (Amazonas) to Peru, from an altitude of ca. 140 m.

IUCN Red List category. *Myrcia scytophylla* is a rare species known to us only from the type collection. Three further authoritatively named collections are available online (speciesLink, 2015), which give an EOO > 200,000 km². The species is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. The only known duplicate of the type of *Myrcia scytophylla* is at G. It is lectotypified over the holotype fragment at F as it is a more representative sample. In the protologue for *Marlierea scytophylla*, Diels described a partially closed calyx in the bud, similar to that of *Marlierea* sect. *Eugeniopsis* Nied., all species of which that were included in the molecular analysis of Lucas et al. (2011: fig. 1) emerging in a single clade (clade 2). In our opinion, the raised midvein of the adaxial leaf surface and the asymmetric inflorescences place this species in *Myrcia* sect. *Aulomyrcia*. Holst (2002) provided further description and suggested an unqualified affinity to *M. grandis*.

111. *Myrcia sessiliflora* McVaugh, Mem. New York Bot. Gard. 18: 105. 1969. TYPE: Venezuela. Amazonas: Cerro Sipapo (Paráque), 20 Dec. 1948, *B. Maguire 27792* (holotype, MICH-1109551!; isotype, NY-00405476!). [Species group B].

Habitat and distribution. *Myrcia sessiliflora* occurs on stream banks, wet cliffs, and precipitous eastern slopes in Amazonas, Venezuela, at altitudes of ca. 1400–1800 m.

IUCN Red List category. *Myrcia sessiliflora* is known only from the two collections cited here, from a very poorly collected area that is also protected, in the Sipapo Forest Reserve (WDPA, 2015). *Myrcia sessiliflora* is assessed as Data Deficient (DD) according to IUCN criteria (2014).

Notes. The fruits of *Myrcia sessiliflora* are almost entirely sessile with a silky pubescence and a circular scar from the hypanthium; superficially, they resemble fruits of the genus *Plinia*. McVaugh (1969) described a folded embryo in this species, confirmed from the isotype at NY. McVaugh cited an affinity of *M. sessiliflora* with 4-merous montane species, such as *M. saxatilis*, in the protologue. We find, however, that the species resembles *M. caudata* and shares a (in this case completely) reduced inflorescence with other species of *Marlierea* sect. *Myrciopsis* (McVaugh, 1958).

Selected specimen. VENEZUELA. **Amazonas:** Cerro Sipapo (Paráque), W Peak, *Maguire & Politi 27908* (MICH).

112. *Myrcia skeldingii* Proctor, Rhodora 60: 325. 1959. TYPE: Jamaica. Parish of Clarendon: Mason River Savannah, 2.75–3 mi. NW of Kellits, 14 Oct. 1957, *G. R. Proctor 16478* (holotype, IJ-19896!; isotypes, A!, US-00117772!, US-00997541!). [Species group B].

Habitat and distribution. *Myrcia skeldingii* is endemic to the Mason River Savannah, Jamaica, at an altitude of ca. 700 m.

IUCN Red List category. *Myrcia skeldingii* is apparently dioecious; this distinctive species is known from two collections (four specimens) from the single Mason River locality, hence a very restricted AOO. The Mason River Savannah is under threat from farming and invasive species, but the type locality falls within the Mason River Reserve. *Myrcia skeldingii* has not been recollected since 1965 and has been considered to be Extinct (EX) (Kelly, 1998) according to IUCN criteria (2014).

Notes. The protologue of *Myrcia skeldingii* mentions an affinity with *M. uberavensis* O. Berg; however, we find much more resemblance to *M. cana* and *M. platyclada*. *Myrcia skeldingii* has subsessile, coriaceous, revolute leaves with flat to gently channeled midveins and dark petioles. The inflorescences are terminal, thick, darkened cymose panicles with flattened rachises and terminal bunches of buds. Buds are turbinate with short calyx lobes that tear the hypanthium into four or five irregularly sized lobes. Fruits resemble continental species with a tubular hypanthial remaining on the fruit.

113. *Myrcia skortzoviana* (Mattos) E. Lucas & C. E. Wilson, comb. nov. Basionym: *Marlierea skortzoviana* Mattos, Loefgrenia 54: 1. 1971, replacement name for *Marlierea subulata* Mattos, Ci & Cult. 19: 332. 1967, nom. illeg., non *Marlierea subulata* McVaugh, Fieldiana, Bot. 29: 177. 1956. TYPE: Brazil. São Paulo: Paranapiacaba, Estação Biológica (via ferrea São Paulo–Santos), s.d., J. R. Mattos 11839 (holotype, SP-80782!). [No species group assignment].

Habitat and distribution. *Myrcia skortzoviana* is found in the mountainous forests of High Serra Paranapiacaba, São Paulo, Brazil, at an altitude of ca. 800 m.

IUCN Red List category. *Myrcia skortzoviana* appears to have a very restricted EOO, and although it was collected in an ecological station, the level of legislation is low; ca. 250 km² of the reserve was destroyed in 1970 for construction of a highway. This species is assessed as Vulnerable (VU D2) according to IUCN criteria (2014).

Notes. *Myrcia skortzoviana* is known to us from the image of the holotype. The species has an incompletely closed calyx in bud; the inflorescence is reduced to distinctive, short, lateral, few-flowered panicles, described in the protologue as simple dichasia. The reduced inflorescence of this species as well as the manner of tearing of the calyx deep into the hypanthium suggests its placement in *Myrcia* sect. *Aulomyrcia*.

114. *Myrcia speciosa* (Amshoff) McVaugh, Mem. New York Bot. Gard. 18: 106. 1969. Basionym: *Aulomyrcia speciosa* Amshoff, Recueil Trav. Bot. Néerl. 42: 5. 1950. TYPE: British Guiana [Guyana.] 115 m Bartica–Potaro Rd., 24 Jan. 1943, D. B. Fanshawe 3836 (holotype, K-000344368!; isotype, U-0008496!). [Species group A].

Habitat and distribution. *Myrcia speciosa* occurs in rocky places on lateritic soil and wet dense forests in Cuyuni-Mazaruni, Guyana, at an altitude of ca. 100 m.

IUCN Red List category. *Myrcia speciosa* is known from three collections, suggesting a small population. This area of Guyana is not well collected, making it difficult to speculate on population size. *Myrcia speciosa* occurs in remote, unprotected primary vegetation under low-level threat from small-scale mining (EOE, 2015); it may be vulnerable to stochastic change. It is assessed as Vulnerable (VU D2) according to IUCN criteria (2014).

Notes. Amshoff (1950) and McVaugh (1969) commented on the difficulty in deducing the relationships of this very distinct and rare species. We tentatively suggest an affinity between *Myrcia speciosa* and other species with raised midveins and terminal inflorescences.

Selected specimen. GUYANA. **Potaro-Siparuni:** Mahdia R., Potaro R., 107 mi. Bartica–Potaro Rd., 8 Jan. 1943, Forest Department of British Guiana 3722 (K).

115. *Myrcia stictophylla* (O. Berg) N. Silveira, Roessléria 7: 66. 1985. Basionym: *Aulomyrcia stictophylla* O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14 (1): 67. 1857. TYPE: [Brazil.] Rio de Janeiro, s.d., F. Sellow s.n. (holotype, B†; lectotype, designated here, P-00798925!; isolectotypes, F-0064771F!, K-000344395!, LE!, P-00161078!, P-00161079!). [No species group assignment].

Habitat and distribution. *Myrcia stictophylla* occurs in the coastal cordillera region of the Atlantic forests of Brazil at an altitude of ca. 30 m.

IUCN Red List category. We presume this species, known from few collections, to have a very restricted population. The species occurs in an ecological station of the Atlantic forest; environmental protection exists but is not strictly enforced. The threats to this biome are many; if legislation was to change, specific threat would be immediate. *Myrcia stictophylla* is assessed as Vulnerable (VU D2) according to IUCN criteria (2014).

Notes. *Myrcia stictophylla* is a poorly known and little-collected species. The material available indicates a species with consistently acuminate leaf tips and terminal inflorescences with thickened rachises.

Myrcia stictophylla has been compared to *M. gilsoniana*; see note under that species.

Selected specimen. BRAZIL. **São Paulo:** Iguape, Estação Ecol. Jureia-Itatins, Trilha para o Pocinho, *Costa* 64 (K).

116. *Myrcia subobliqua* (O. Berg) Nied., Nat. Pflanzenfam. 3(7): 76. 1893. Basionym: *Aulomyrcia subobliqua* O. Berg, Linnaea 27: 57. 1855. TYPE: [Guyana] British Guiana. Piarra ad al flumen Essequibo, s.d., *R. Schomburgk* 597 (holotype, B†; lectotype, designated here, K-000344434!; isoelectotypes, BM!, BR-0000005289080!, E-00394773!, F-0065330F!, F-0065331F!, F-0065332F!, GH-00069397!, K-000344436!, MICH-1109627!, NY-00405028!, P-00552202!, P-00552600!, US-00048581!). [Species group C].

Habitat and distribution. *Myrcia subobliqua* occurs on river margins of low-altitude, ombrophilous forest, reported from Guyana, Suriname, French Guiana, and Brazil from altitudes of ca. 10–180 m.

IUCN Red List category. *Myrcia subobliqua* is a well-collected species with an EOO > 130,000 km². It is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia subobliqua* is a larger-leaved (to 20 cm) species associated with *M. pyrifolia* by McVaugh (1969), despite his classification of them in separate sections. The inflorescence of *M. subobliqua* comprises large, mostly regular triangular panicles in terminal and subterminal leaf axes. Leaf midveins are raised, and calyx lobes are pubescent within. This species is newly recorded from Brazil.

Selected specimens. BRAZIL. **Amapá:** rd. betw. Calcoene & Oiapoque (BR-156) 7 km SSE of Oiapoque, *Rabelo* 2870 (K). **Roraima:** 1843, *Schomburgk* 386 (K). GUYANA. **Cuyuni-Mazaruni:** Essequibo River betw. Omai & Dennison Mine, *Gillespie* 1431 (K). **Takutu-Upper Essequibo:** 5 km upstream from Kurupukari, right bank, *Pennington* 374 (K). SURINAME. **Sipaliwini:** N side of Kuruni Island, 30 km E of confluence on Corantijn River, *Evans* 1928 (K).

117. *Myrcia suborbicularis* (McVaugh) E. Lucas & C. E. Wilson, comb. nov. *Marlierea suborbicularis* McVaugh, Mem. New York Bot. Gard. 10(1): 88. 1958. TYPE: Venezuela. Amazonas: Rio Guainia, in sabanita 1 km E of Maroa, 25 Nov. 1953, *B. Maguire* 36400 (holotype, MICH-1109460!; isotypes, F-0065398F!, US-00036834!, VEN-41600!). [Species group B].

Habitat and distribution. *Myrcia suborbicularis* is endemic to Venezuela (Amazonas) and is associated with waterways in low forests on white sandy savanna at an altitude of ca. 110 m.

IUCN Red List category. Known to us only from the type collection but with seven further authoritatively identified species listed online (TROPICOS®, 2015), this species has an EOO of ca. 14,000 km² and is known from less than 10 localities, both criteria giving this species a Vulnerable category according to the IUCN criteria (2014). However, the collection localities lie within the Guianan and Negro-Branco moist forest ecoregions (WWF, 2014) that are under relatively low threat (EOE, 2015). Therefore, *Myrcia suborbicularis* does not completely fulfill criterion B of the IUCN (2014) and is assessed as Least Concern (LC).

Notes. *Myrcia suborbicularis* is a shrubby species with rounded, subsessile leaves, flattened rachises, and cymose inflorescences. The protologue states that there is an affinity with *M. neomontana* and that *M. suborbicularis* has three to five ovules per locule, which is unusual for *Myrcia* sect. *Aulomyrcia*.

118. *Myrcia subulata* (McVaugh) E. Lucas & C. E. Wilson, comb. nov. Basionym: *Marlierea subulata* McVaugh, Fieldiana, Bot. 29: 177. 1956. TYPE: Peru. Loreto: Mishuyacu, near Iquitos, May 1930, *G. Klug* 1341 (holotype, F-0040044F!; isotypes, NY-00405305!, US-00036833!). [No species group assignment].

Habitat and distribution. *Myrcia subulata* has been collected from river margins of low-altitude, ombrophilous forest from southern Venezuela to Bolivia at an altitude of ca. 100 m.

IUCN Red List category. *Myrcia subulata* is a well-collected species with an EOO > 900,000 km². *Myrcia subulata* is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia subulata* resembles *M. fusca* from Panama with its subcordate, large (to ca. 30 cm) leaves with channeled midveins adaxially and terminal inflorescences with long opposite axes (not whorled); it differs from *M. fusca* in having less bullate, larger leaves. Holst (2002) provided further description and many additional specimen citations.

Selected specimens. BOLIVIA. **Pando:** W bank of Río Madeira, 2 km above Riberão Forest, *Prance* 6480 (K). BRAZIL. **Amazonas:** Rio Curuquete, halfway betw. Cachoeira São Paulo & República, *Prance* 14509 (K).

Rondônia: N bank of Rio Abuna, betw. cachoeira Tres S & Fortaleza, 4–16 km above mouth, *Prance 6168* (K). PERU. **Loreto:** Maynas, Quebrada Santa Cruz, *Vasquez 2959* (K); along the Ucalayi River, ca. 7 km SW of Jenaro Herrera village, Zone de Lobillo, near Nuevo Aucayacu, *Kvist 1039* (K).

119. *Myrcia sucrei* (G. M. Barroso & Peixoto) E. Lucas & C. E. Wilson, comb. nov. Basionym: *Marlierea sucrei* G. M. Barroso & Peixoto, Acta Bot. Brasil. 4(2): 15. 1990. TYPE: [Brazil.] Espírito Santo: Linhares, 31 Jan. 1972, *D. Sucre 8320* (holotype, CVRD not seen; isotypes, NY-01546322!, RB-00542137!, RBR not seen). [Species group E].

Habitat and distribution. *Myrcia sucrei* is found in the Atlantic forest of eastern Brazil from tabuleiro vegetation (from southeastern Bahia, Espírito Santo) at altitudes of ca. 0–500 m.

IUCN Red List category. *Myrcia sucrei* has an EOO > 900,000 km², which is sufficient to avoid a category of threat. The species is protected in the Vale do Rio Doce reserve in Espírito Santo. *Myrcia sucrei* is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia sucrei* has large, leathery leaves with a convex midvein above. The inflorescence is made up of multiple terminal spikes that bear sessile flowers. The axes of the inflorescence, the bracts, and the external surfaces of flowers are covered in long, golden hairs. Large (to 3 mm), pubescent bracts subtend every flower; the flowers are internally glabrous.

Selected specimens. BRAZIL. **Bahia:** Km. 17 da estrada que liga a Rod. BR 101 (São Jose) a Rod. BA-215, *Mori 11723* (K). **Espírito Santo:** Linhares, Comp. Vale do Rio Doce, estrada Mantegueira, Res. Linhares, *Lucas 840* (K).

120. *Myrcia tetraphylla* Sobral, J. Bot. Res. Inst. Texas 4: 152. 2010. TYPE: Brazil. Southern Bahia: Ilhéus, Una, 26 Aug. 1993, *J. Jardim 265* (holotype, CEPEC58815 not seen; isotypes, NY-00615552!, RB-00314569!). [Species group A].

Habitat and distribution. *Myrcia tetraphylla* is known from the rainforests of coastal Bahia at altitudes of ca. 0–100 m.

IUCN Red List category. The protologue of *Myrcia tetraphylla* (Sobral, 2010) assessed it as Endangered (EN) according to IUCN criteria (2014).

Notes. The protologue (Sobral, 2010) of *Myrcia tetraphylla* stated affinities with *M. clavija* and *M. eumecephylla* based on leaf disposition. This species was differentiated in having petioles to 20 mm, leaf bases attenuate, and fruit to 22 mm in diameter; the calyx lobes were not aristate.

Selected specimen. BRAZIL. **Bahia:** Ilhéus, Estrada entre Sururu e Vila Brasil, a 6–14 km de Sururo, a 12–20 km SE de Buerarema, *Mori 12887* (K).

121. *Myrcia umbraticola* (Kunth) E. Lucas & C. E. Wilson, comb. nov. Basionym: *Myrtus umbraticola* Kunth in F. W. H. A. von Humboldt, A. J. A. Bonpland & C. S. Kunth, Nov. Gen. Sp. 7: 258. 1825. *Marlierea umbraticola* (Kunth) O. Berg in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 14: 35. 1857. TYPE: [Brazil. Amazonas:] Maypures, s.d., F. W. H. A. Von Humboldt & Bonpland s.n. (holotype, P-00679482!). [Species group C].

Habitat and distribution. *Myrcia umbraticola* is known from forests and shady riverbanks of the Orinoco and Casiquiare Rivers of Colombia and Venezuela into Amazonian Brazil at altitudes of ca. 100–140 m.

IUCN Red List category. *Myrcia umbraticola* has an EOO > 1 million km². *Myrcia umbraticola* is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia umbraticola* is a widely distributed and well-collected species that appears to comprise multiple entities. The type specimen is sterile but shows a larger-leaved, brown-drying species with open blade venation and smooth petioles. Herbarium material of a separate entity attributed to this name has smaller (no more than 5 cm), discoloured leaves with finer, closed secondary venation to the blades; petioles are often corky (e.g., *Cid 4066*, K). Future studies may support this as a separate species. Calyx lobes are internally pubescent on both forms.

Selected specimens. BRAZIL. **Amapá:** betw. Calcoene & Oiapoque, 110 km NW of Calcoene, *Rabelo 2940* (K). **Amazonas:** Rio Abacaxia, igarapé Cuera, *Cid 4066* (K); Reserva Flor. Ducke, Manaus–Itacoatiara, Km. 26, *de Souza 110* (K). **Pará:** Jari, Estrada entre Planalto A e Braco, *Silva 1835* (K). GUYANA. Upper Takutu–Upper Essequibo, *Clarke 3605* (U). VENEZUELA. In Vasurie, *Spruce 3316* (K).

122. *Myrcia uniflora* (McVaugh) E. Lucas & C. E. Wilson, comb. nov. Basionym: *Marlierea uniflora* McVaugh, Mem. New York Bot. Gard. 18:

69. 1969. TYPE: Venezuela. Amazonas: Río Guiana, 14 Oct. 1957, *B. Maguire 41888* (holotype, MICH-1109452!; isotypes, NY-00405311!, S-052574!, US-00117795!, VEN-76123!). [No species group assignment].

Habitat and distribution. *Myrcia uniflora* is known from savanna regions of southern Venezuela into northern Brazil at altitudes of ca. 20–140 m.

IUCN Red List category. *Myrcia uniflora* is known to us only from the type collection. Authoritatively named specimens online (TROPICOS®, 2015) have been collected from an area that suggests an EOO of ca. 20,000 km² within the Negro Branco ecoregion (WWF, 2014) that is under relatively low environmental threat. The species is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia uniflora* is a poorly known species but one that is distinctive in having uniflorous inflorescences. The flowers are closed in bud and tear open into three to four reasonably equal calyx lobes. McVaugh (1969) noted a similarity to small-leaved *Marlierea* and *Calyptranthes* with bicarinate branchlets. This species may be affiliated with those of *Marlierea* sect. *Myrciopsis* (McVaugh, 1958). Holst (2002) provided further description and additional specimen citations.

Selected specimen. BRAZIL. **Amazonas:** São Gabriel da cachoeira, Rio Cubate, afluente do Içana, *Farney 1886* (K).

123. *Myrcia ventuarensis* (B. Holst) E. Lucas & C. E. Wilson, comb. nov. Basionym: *Marlierea ventuarensis* B. Holst, *Selbyana* 23: 152. 2002. TYPE: Venezuela. Amazonas: Atabapo, Cerro Moriche, Oct. 1989, *L. Delgado 893* (holotype, PORT-65583!; isotypes, NY not seen, SEL-003101!, VEN-211655!). [Species group B].

Habitat and distribution. *Myrcia ventuarensis* has been collected from shrubby savannas or scrub forests in southern Venezuela at altitudes of 200–350 m.

IUCN Red List category. *Myrcia ventuarensis* is known only from the type and one further authoritatively named specimen (TROPICOS®, 2015) from the Rio Ventuari. These sites form part of the Negro Branco moist forest ecoregion, said to be under low environmental threat due to its inaccessibility (WWF,

2014). The species is assessed as Data Deficient (DD) according to IUCN criteria (2014).

Notes. Holst (2002) suggested an unqualified affinity of *Myrcia ventuarensis* with *M. neoschomburgkiana* but distinguishes the former species on the basis of its shallowly sulcate (vs. raised) midveins, mostly elliptic (vs. obovate) blades, and impressed-punctate (vs. not impressed-punctate) adaxial leaf surfaces.

124. *Myrcia zetekiana* (Standl.) B. Holst, *Novon* 15: 296. 2005. Basionym: *Eugenia zetekiana* Standl., *J. Wash. Acad. Sci.* 15: 286. 1925. *Aulomyrcia zetekiana* (Standl.) Amshoff, *Ann. Missouri Bot. Gard.* 45: 170. 1958. TYPE: Panama. Canal Zone: in wet forest on hills N of Frijoles, 19 Dec. 1923, *P. C. Standley 27503* (holotype, US-00008153!; isotypes, BM-000645689!, K-000261052!). [Species group A].

Habitat and distribution. *Myrcia zetekiana* is known from wet forests of Panama and is also reported from Colombia, at an altitude of ca. 100 m.

IUCN Red List category. Authoritatively named specimens of *Myrcia zetekiana* recorded online suggest an EOO for this species of ca. 1500 km². Panamanian collections are from well-protected areas such as the Bosque de proteccion Lago Gatun, Soberania Parque Nacional, and Chargres Parque Nacional. *Myrcia zetekiana* is assessed as Least Concern (LC) according to IUCN criteria (2014).

Notes. *Myrcia zetekiana* has distinctive large leaves (to 30 cm) and large flowers (to 0.5 cm) as well as pubescent fruits. This species has been relatively well collected, although we have seen little material.

Selected specimen. PANAMA. Canal Zone, Hills W of the canal, near Gatun, *Standley 27192* (K).

INCOMPLETELY KNOWN SPECIES

We believe the following species may additionally be included in *Myrcia* sect. *Aulomyrcia* but lack sufficient data for certain placement. The holotypes of *Marlierea involucrata* (O. Berg) Nied. and *Myrcia panicularis* (O. Berg) N. Silveira were destroyed in B, and with no syntypes, specimens contemporary with the author, or other reliably named material available for reference, it is impossible to understand Berg's original concepts of these species and to provide

lectotypification or confidently place the species, though their protologues suggest they belong to *Myrcia* sect. *Aulomyrcia*. *Myrcia calycampa* Amshoff, *M. elevata* M. F. Santos, *M. gonini* McVaugh, *M. intonsa* (McVaugh) B. Holst, *M. ramageana* Krug & Urb., and *M. tafelbergica* Amshoff form a group of species from the Amazon basin and Caribbean with short pale to rufous hairs covering hypanthia and axes of the inflorescence. Holst (2002) discusses a calycampe complex that may correspond in some way to these species. It is difficult to assess the buds and flowers of these species from available material and images. They appear to have the flat disk and thick, hairy staminal ring associated with *Myrcia* sect. *Myrcia*; however, in fruit the hypanthium can extend significantly and tear. It will be important to include samples of them in future molecular-based analyses and equally important to bear these species in mind when considering further accounts of *Myrcia* sect. *Aulomyrcia*.

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THE GENUS *GLANDULARIA* (VERBENACEAE) IN BRAZIL¹

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ABSTRACT

Glandularia J. F. Gmel. (Verbenaceae) is the largest genus in the tribe Verbenae, with ca. 84 species distributed mainly in temperate North and South America. A complete taxonomic revision of *Glandularia* in Brazil is provided. Thirty-one species and one variety are present in Brazil, 11 of these being endemic, principally in the southern area of the country. A detailed morphological description is given for each taxon as well as a key for their identification, illustrations, synonymy, distribution, lists of selected specimens, and discussions about the relationships among closely related taxa. A new combination, *G. tomophylla* (Briq.) N. O'Leary & V. Thode, is here proposed, six new synonyms are suggested, and two lectotypes are designated for *Verbena chamaedryfolia* Juss. f. *strigosa* Chodat and *V. humifusa* Cham.

Key words: Brazil, flora, *Glandularia*, taxonomy, *Verbena*, Verbenaceae.

Glandularia J. F. Gmel. (Verbenaceae) is an exclusively American genus with approximately 84 species (Peralta, 2009; Múlgura et al., 2012). In South America, the greatest species diversity is found in the temperate areas of southern Brazil and northern Argentina. It belongs to tribe Verbenae Schauer along with the related genera *Verbena* L., *Junellia* Moldenke, and *Mulguraea* N. O'Leary & P. Peralta (Marx et al., 2010; O'Leary et al., 2012). *Glandularia* species are herbs or suffruticose plants, erect, prostrate or decumbent, mostly with ascending floral branches. *Glandularia* is distinguished from *Verbena*, its sister genus, by the presence of a long style and glandular appendages in the upper pair of stamens, hence the name “*Glandularia*.” However, some species may not contain all of these characters. In addition, the basic chromosome number in *Glandularia* is $x = 5$ and in *Verbena* is $x = 7$ (O'Leary & Peralta, 2007).

In South America *Glandularia* has been recently treated regionally for Argentina (Peralta & Múlgura, 2011) and Chile (O'Leary et al., 2013b). At the moment, apart from the Brazilian flora checklist (Thode & O'Leary, 2014) no complete treatment for *Glandularia* in Brazil exists. The only known floristic study for the genus in the country is for the state of Rio Grande do Sul where the authors mentioned 27 species (Thode & Mentz, 2010). Therefore, the present contribution represents the first complete taxonomic revision of genus *Glandularia* for Brazil.

MATERIALS AND METHODS

This taxonomic revision is based on collections from the following herbaria: CESJ, CTES, ESA, HBR, HPL, ICN, LIL, LP, MBM, NY, PACA, SI, and UFPR (Thiers, 2013). Following the herbaria initials is the herbarium sheet number or the barcode number (bc). When the specimen was seen, it is indicated by an exclamation mark. When the digital photo of the specimen was seen in JSTOR (<http://plants.jstor.org/>) or in virtual herbaria, it is indicated by “image!”

Flower measurements were taken from dried material that had been rehydrated by boiling. Fruit measurements were taken from dried specimens. The descriptive terminology of the inflorescences used here is in accordance with Múlgura et al. (2002), the morphological terms follow Hickey (1974), and the descriptions of pubescence follow Lawrence (1951). The taxa distribution and habitat data were taken from the herbarium specimen labels.

Only Brazilian specimens are cited in the examined material, and only one specimen per state is cited. The accepted names are listed in Appendix 1, and a list of the taxa synonymized in the present work, with indication of their actual taxonomic position, is presented in Appendix 2.

TAXONOMIC TREATMENT

Glandularia J. F. Gmel., Syst. Nat., ed. 13 [bis] 2(2): 886, 920. 1791 [1972]. *Verbena* L. subg. *Glandularia* (J. F. Gmel.) Nutt., J. Acad. Nat.

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Sci. Philadelphia 2(1): 123. 1821. *Verbena* sect. *Glandularia* (J. F. Gmel.) Schauer, Prodr. [DC.] 11: 550. 1847. *Verbena* subg. *Glandularia* (J. F. Gmel.) W. H. Lewis & R. L. Oliv., Amer. J. Bot. 48: 638–642. 1961, nom. illeg. hom. TYPE: *Glandularia carolinensis* J. F. Gmel. [= *Glandularia canadensis* (L.) Nutt., nom. illeg.].

Shuttleworthia Meisn., Pl. Vasc. Gen. 1: 290. 1840.

Uwarowia Bunge, Bull. Sci. Acad. Imp. Sci. Saint-Petersbourg 7: 278. 1840.

Verbena ser. *Nobilis* Schauer, Prodr. [DC.] 11: 537. 1847.

Herbs or suffruticose plants, prostrate or erect, stems erect or decumbent with ascending floral branches. Stems cylindrical to 4-angled. Leaves simple, opposite, blade entire, linear, elliptic, oblong, obovate or ovate, or divided, 3- to 5-lobed, 3- to 5-parted, 3- to 5-dissected, 2-pinnatipartite or 2- to 3-pinnatisect; sessile, subsessile or petiolate; apex acute or round, base attenuate, acute or truncate; margins entire, crenate, serrate, dentate or lobed; pubescence glabrous to variously strigose, hispid, hirsute, with or without glandular hairs. Inflorescences globose or spicate in anthesis, elongated or not in fructification, sessile or peduncled, grouped (pleiobotrya) in terminal (heterothetic) position or solitaire (monobotrya). Flowers sessile to subpedicellate, subtended by elliptic or ovate floral bracts. Calyx with 5 unequal teeth, aristate, acute, triangular, or almost mucronate, variable in length, external surface glabrous to variously pubescent: strigose, hirsute or hispid, sometimes retrorse hairs, with glandular hairs present or not, sometimes with patelliform glands, internal surface glabrous; fully accrescent in fruit and persistently enclosing mature schizocarp. Corolla hippocrateriform, white, violet, blue, pink, lilac, pale

blue, or red; tube cylindrical, externally glabrous to variously pubescent, internally villous along distal half; limb 5-lobed, lobes emarginate. Androecia composed of 4 didynamous stamens, thecae longitudinally dehiscent, superior pair with or without glandular anther connective appendages, sometimes surpassing the thecae, and weakly exerted from the corolla mouth. Gynoecia composed of a bicarpellate ovary 2-locular, with 2 ovules per carpel, style filiform, generally more than 3 times the length of the ovary, rarely shorter, stigma bilobed. Dry schizocarpic fruit, composed of 4 cylindrical cluses, apex round or rostrate, dorsal surface reticulate to plane, ventral surface papillose to verrucose. Base chromosome number $x = 5$.

Distribution and ecology. *Glandularia* is an American genus comprising ca. 84 species (Peralta, 2009) with a disjunct distribution, growing in North America, from the southern United States and Mexico to Guatemala, and in South America, in Brazil, Peru, Bolivia, Paraguay, Chile, Argentina, and Uruguay. It is found from sea level up to 4600 m elevation, in the Andean region.

Brazil has great species diversity with 32 taxa distributed from sea level up to 2000 m in the southern and southeastern Brazilian mountain ranges. The *Glandularia* species are found in southern Brazilian states, with records from Rio Grande do Sul, Santa Catarina, Paraná, São Paulo, Rio de Janeiro, Minas Gerais, and Mato Grosso do Sul. Rio Grande do Sul exhibits the greatest specific diversity, with 26 species and one variety. They occur in grasslands, rocky fields, sand, flooded areas, roadsides, hillsides, forests, and forest margins.

KEY TO SPECIES OF *GLANDULARIA* FROM BRAZIL

- 1. Leaf blades entire, margin lobed, serrate, dentate, or entire 2
- 1'. Leaf blades not entire, lobate, parted, dissected, margin entire or dentate 21
- 2(1). Inflorescences arranged in pleiobotrya with bracteose paracladia 3
- 2'. Inflorescences arranged in monobotrya or in frondose pleiobotrya 4
- 3(2). Trimerous or tetrameous disposition of paracladia, calyx less than 5 mm, corolla less than 7 mm 14. *G. lobata* (Vell.) P. Peralta & V. Thode
- 3'. Distal paracladia agglutinated in a corymbiform aspect, calyx longer than 5 mm, corolla longer than 9 mm.... 5. *G. corymbosa* (Ruíz & Pav.) N. O'Leary & P. Peralta
- 4(2'). Leaf blades linear to narrowly elliptic, margin entire or slightly serrate 5
- 4'. Leaf blades elliptic, triangular, ovate, obovate, never narrow, margin never entire, always dentate, serrate, or lobate, if narrowly ovate then with serrate, crenate, or lobate margin 6
- 5(4). Leaf base decurrent, floral bracts 10–14 mm long 26. *G. stellarioides* (Cham.) Schnack & Covas
- 5'. Leaf base cuneate, floral bracts 5–7 mm long 25. *G. sessilis* (Cham.) Tronc.
- 6(4'). Corollas white at anthesis; plants with densely hirsute-glandular pubescence on the stems, leaves, floral bracts, calyx, and corollas 21. *G. platensis* (Spreng.) Schnack & Covas
- 6'. Corollas never white at anthesis; plants never densely hirsute-glandular 7
- 7(6'). Inflorescences paucifloral, corollas up to 6 mm long ... 13. *G. jordanensis* (Moldenke) N. O'Leary & P. Peralta
- 7'. Inflorescences multifloral, corollas more than 10 mm long 8
- 8(7'). Inflorescences not enlarged in fructification 9
- 8'. Inflorescences enlarged in fructification 11
- 9(8). Plants with strigose pubescence on stems and calyx; the calyx with patelliform glands 16. *G. megapotamica* (Spreng.) Cabrera & G. Dawson

9’.	Plants with hirsute-glandular or hispid, sometimes glandular, pubescence on stems and calyx	10
10(9’).	Plants glandular-hirsute, floral bracts narrowly ovate, 5–6 mm long, calyx teeth acute, 1–2 mm long.....	
 20. <i>G. phlogiflora</i> (Cham.) Schnack & Covas	
10’.	Plants hirsute, sometimes glandular; floral bracts ovate, 1.5–3 mm long, calyx teeth brief triangular, 1–1.2 mm long.....	8. <i>G. guaranitica</i> Tronc.
11(8’).	Leaves glabrous on both surfaces; stamens with glandular appendages, surpassing the thecae, slightly surpassing the corolla mouth	11. <i>G. herteri</i> (Moldenke) Tronc.
11’.	Leaves never glabrous, variously pubescent; stamens with or without glandular appendages	12
12(11’).	Leaf blades 3-lobed; corollas externally glabrous	12. <i>G. humifusa</i> (Cham.) Botta
12’.	Leaf blades entire; corollas externally villous, never completely glabrous	13
13(12’).	Leaf blades obovate; obtuse apex	15. <i>G. marrubioides</i> (Cham.) Tronc.
13’.	Leaf blades ovate, elliptic, triangular, never obovate; acute or subobtuse apex	14
14(13’).	Non-glandular pubescence on floral bract and calyx	15
14’.	Glandular pubescence on floral bract and calyx	17
15(14).	Cluses with rostrate apex, calyx teeth 2–4 mm long	9. <i>G. hasslerana</i> (Briq.) Tronc.
15’.	Cluses with round apex, calyx teeth shorter than 2 mm long	16
16(15’).	Superior pair of stamens unappendaged	18. <i>G. paulensis</i> (Moldenke) A. L. R. Oliveira & Salimena
16’.	Superior pair of stamens with glandular appendages, surpassing thecae, not surpassing corolla mouth	19
17(14’).	Leaf blades ovate triangular, petiole 8–25 mm long	18
17’.	Leaf blades elliptic to ovate, if triangular then briefly petiolated, petiole shorter than 8 mm	20
18(17).	Cluses rostrate, 4–6 mm long	17. <i>G. nana</i> (Moldenke) Tronc.
18’.	Cluses rounded, 2.8–3 mm long	23. <i>G. scrobiculata</i> (Griseb.) Tronc.
19(16’).	Calyx teeth acute, 1.8 mm long	30. <i>G. tomophylla</i> (Briq.) N. O’Leary & V. Thode
19’.	Calyx teeth brief, triangular, 0.5 mm long	7. <i>G. guaibensis</i> P. Peralta & V. Thode
20(17’).	Corollas bright red	19. <i>G. peruviana</i> (L.) Small
20’.	Corollas lilac or pink, exceptionally white	31. <i>G. tweedieana</i> (Niven ex Hook.) P. Peralta
21(1’).	Inflorescences not showy, corollas brief, less than 7.5 mm	22
21’.	Inflorescences showy, corollas long, more than 10 mm	24
22(21).	Leaves 3-parted, segments lobed to parted	10. <i>G. hatschbachii</i> (Moldenke) N. O’Leary & P. Peralta
22’.	Leaves 3-dissected, segments linear or narrowly elliptic	23
23(22’).	Leaves 5–10 mm long; floral bracts 1.8–3 mm; calyx 3–4 mm long; corolla tube 4–5.5 mm long.....	
 29. <i>G. thymoides</i> (Cham.) N. O’Leary	
23’.	Leaves 10–20 mm long; floral bracts 3–6.5 mm; calyx 4.5–7.5 mm long; corolla tube 5.5–8 mm long....	
 3. <i>G. balansae</i> (Briq.) N. O’Leary	
24(21’).	Superior pair of stamens with glandular appendages, surpassing corolla mouth	25
24’.	Superior pair of stamens unappendaged or with glandular appendages but not surpassing corolla mouth	27
25(24).	Cluses rostrate	31
25’.	Cluses round	26
26(25’).	Corollas externally villous	24. <i>G. selloi</i> (Spreng.) Tronc.
26’.	Corollas externally glabrous	27. <i>G. subincana</i> Tronc.
27(24’).	Corollas externally glabrous, leaves 3-dissected to bi- to tri-pinnatisect	28
27’.	Corolla externally villous, leaves lobate, pinnatilobate, 3-parted to 3-dissected, sometimes pinnatisect at apical nodes	29
28(27).	Calyx 9–10 mm long; superior pair of stamens with glandular appendages, not surpassing corolla mouth; cluses 3 mm long	2. <i>G. aristigera</i> (S. Moore) Tronc.
28’.	Calyx 15–20 mm long; superior pair of stamens unappendaged; cluses 4.5–5 mm long.....	
 1. <i>G. angustilobata</i> (Moldenke) P. Peralta & V. Thode	
29(27’).	Abaxial foliar surface, floral bract, and calyx with glandular hairs, calyx teeth triangular, less than 1 mm long	4. <i>G. catharinae</i> (Moldenke) N. O’Leary & P. Peralta
29’.	Abaxial foliar surface, floral bract, and calyx with no glandular hairs; calyx teeth acute or aristate, more than 1.5 mm long	30
30(29’).	Calyx surface evenly hispid, floral bracts 3–5 mm long, narrowly ovate, acute apex, strigose, cluse with round apex	30. <i>G. tomophylla</i> (Briq.) N. O’Leary & V. Thode
30’.	Calyx surface hispid only on nerves, floral bracts 4.5–8 mm long, widely ovate, acute apex, glabrous, cluse with rostrate apex	6. <i>G. dusenii</i> (Moldenke) N. O’Leary & P. Peralta
31(25).	Leaves 3-dissected, rarely bipinnatisect, 30–55 × 20–40 mm, petiole 11–15 mm, corolla 14–18 mm	
 22. <i>G. rectiloba</i> (Moldenke) P. Peralta & V. Thode	
31’.	Leaves 3- to 5-dissected to bipinnatisect, 15–20 × 15 mm, petiole less than 10 mm, corolla 12–13 mm	28. <i>G. tenera</i> (Spreng.) Cabrera

1. *Glandularia angustilobata* (Moldenke) P. Peralta & V. Thode, *Rodriguésia* 61(suppl.): 30. 2010. Basionym: *Verbena cabreræ* Moldenke var. *angustilobata* Moldenke, *Phytologia* 28: 195. 1974. TYPE: Brazil. Mato Grosso do Sul: Mun.

Aquidauana, cerrado at Col. Paxixi, 20 Feb. 1973, *G. Hatschbach* 23852 (holotype, TEX [bc] TEX375217!; isotype, MBM!, SI!). Figure 1.

Erect to prostrate herb, stems erect or decumbent with ascending floral branches, pubescence strigose.

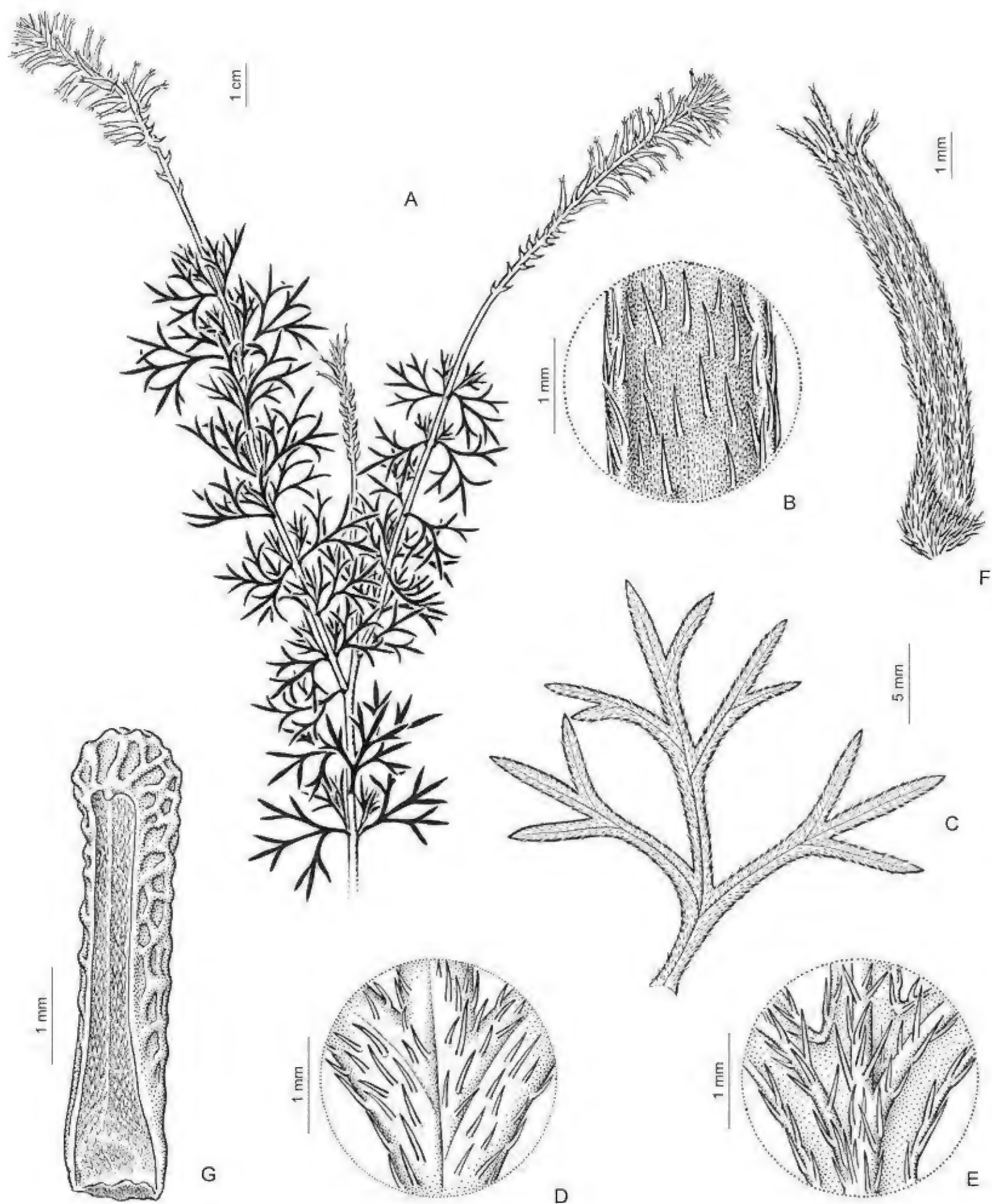


Figure 1. *Glandularia angustilobata* (Moldenke) P. Peralta & V. Thode. —A. Floriferous branch, general aspect. —B. Detail of stem pubescence. —C. Leaf, adaxial surface. —D. Detail of leaf pubescence, adaxial surface. —E. Detail of leaf pubescence, abaxial surface. —F. Calyx and floral bract. —G. Cluse, ventral face. A–G from *Krapovichkas* 32877 (Sl).

Leaves briefly petiolate, petiole less than 10 mm, blade 25–30 × 20–25 mm, 3-sected to bipinnatisect, both surfaces strigose, margin revolute. Inflorescences arranged in frondose pleiobotrya, lateral paracladia surpassing terminal florescence, florescences represented by dense multifloral spikes, enlarged in fruit, peduncles 25–50 mm.

Floral bracts 2.5–4 mm, ovate, apex aristate, pubescence strigose, sometimes with patelliform glands. Calyx 15–20 mm, the surface strigose with some patelliform glands, teeth acute, 1.8 mm. Corolla 12–13 mm, externally glabrous, violet. Superior pair of stamens unappendaged, style 9–10 mm. Cluses 4.5–5 mm, apex round.

Distribution. *Glandularia angustilobata* is endemic to the Brazilian state of Mato Grosso do Sul.

Notes. *Glandularia angustilobata* is similar to *G. aristigera*. They differ by the calyx size, which is 15–20 mm long in *G. angustilobata* and less than 10 mm long in *G. aristigera*. In *G. angustilobata*, the stamens are unappendaged and the cluses are bigger (4.5–5 mm) than those in *G. aristigera* (3 mm).

Selected specimens examined. BRAZIL. **Mato Grosso do Sul:** 23 km de Aquidauana, Krapovickas 32877 (SI).

2. *Glandularia aristigera* (S. Moore) Tronc., Darwiniana, 14: 636. 1968. Basionym: *Verbena aristigera* S. Moore, Trans. Linn. Soc. London, Bot. ser. 2, 4: 439. 1895. TYPE: Brazil. Mato Grosso do Sul: “Prope montem Pão d’Assucar dictum, inter Coimbrá et fl. Apa,” 1891–1892, S. Moore 1083 (lectotype, designated by Peralta & Múlgura [2011: 368], BM [bc] BM0000070617!; islectotype, SI [bc] 00003677!). Figure 2.

Verbena tenuisecta Briq., Annuaire Conserv. Jard. Bot. Genève 7–8: 294. 1904. *Glandularia tenuisecta* (Briq.) Small, Man. Southeast. Fl.: 1139. 1933. TYPE: Paraguay. La Trinidad: 4-X-1875, B. Balansa 1025 (holotype, G [bc] G00077154!, isotypes, F [bc] F0074536!, G [bc] G000077155!, K [bc] K000470520!, NY [bc] KNY138336!, P [bc] P0000650869!, P [bc] P0000650868!, SI!).

Verbena cochabambensis Moldenke, Castanea 10: 45. 1945. TYPE: Bolivia. Cochabamba: Maica, 2500 m, Mar. 1941, M. Cárdenas 2212 (holotype, NY [bc] NY00138256!; isotypes, SI [bc] SI00003819!, US [bc] US0000118683!).

Prostrate herb, 15–60 cm tall, stems decumbent with ascending floral branches, pubescence glabrous to strigose. Leaves briefly petiolate, petiole less than 10 mm, blade 10–30 × 15–30 mm, 3-dissected to bi- to tri-pinnatisect, segments linear to ovate, both surfaces strigose, margin revolute. Inflorescences arranged in monobotrya or frondose pleiobotrya, lateral paracladia surpassing the terminal florescence, inflorescences represented by dense, multifloral spikes, enlarged in fruit, peduncle 10–70 mm. Floral bracts 3–4 mm, ovate, apex acute, pubescence strigose, sometimes with patelliform glands. Calyx 9–10 mm, the surface strigose with some patelliform glands, teeth aristate, 0.5–1 mm. Corolla 12 mm, externally glabrous, violet, lilac, or pink. Superior pair of stamens with glandular appendages, surpassing the thecae or not, not surpassing corolla mouth, style 8.5–9 mm. Cluses 3 mm, apex round.

Distribution and ecology. *Glandularia aristigera* is found in northern, northeastern, and central

Argentina, southwestern Bolivia, Paraguay, and southern Brazil. It is probably also present in Uruguay. It inhabits open areas, disturbed areas, roadsides, sand, wetlands, and rocky outcrops, up to 1250 m.

Notes. *Glandularia aristigera* is similar to *G. angustilobata*; see notes under that species. In *G. aristigera* the width of the foliar segments is variable, from linear, as in *G. tenera*, to ovate, as in *G. selloi*. *Glandularia tenera* is distinguished by its rostrate cluses and long stamens with glandular appendages surpassing the corolla mouth, while *G. aristigera* has cluses with a round apex and glandular appendages included. In *G. selloi* the corolla is externally villous, while in *G. aristigera*, *G. angustilobata*, and *G. tenera*, it is glabrous.

Selected specimens examined. BRAZIL. **Mato Grosso do Sul:** Bela Vista, Rio Apa, Hatschbach 58800 (CTES). **Paraná:** Guarapuava, Rio Iguaçu, Barra do Jordão, Hatschbach 9946 (SI). **Rio Grande do Sul:** Santo Angelo, Schulz 465 (SI). **Santa Catarina:** s. loc., Pomerode, H. Lorenzi 1213 (HPL 11325). **São Paulo:** Piracicaba, H. Lorenzi 1972 (HPL 8108).

3. *Glandularia balansae* (Briq.) N. O'Leary, Novon 17: 506. 2007. Basionym: *Verbena balansae* Briq., Annuaire Conserv. Jard. Bot. Genève 7–8: 293. 1904. TYPE: Paraguay. Campos Caaguazú, Mar. 1876, B. Balansa 1028 (lectotype, designated by O'Leary et al. [2007a: 506], G [bc] G00072170!; isotypes, F [bc] F0074499!, K [bc] K0000470519!, P [bc] P0000650819!, SI [bc] SI00003916!). Figure 3.

Plants suffruticose, up to 50 cm tall, stems and branches erect, sometimes decumbent at the base, strigose with scattered glandular hairs. Leaves sessile, blade (5–)10–20 × 0.2–1 mm, trisect, segments linear or narrowly elliptic, lateral segments usually bisected, apex acuminate, margins entire, usually revolute, with scattered short hairs and strigose pubescence on both surfaces and margins. Inflorescences arranged in monobotrya or frondose pleiobotrya, lateral paracladia surpassing the terminal florescence, inflorescences represented by dense multifloral or paucifloral spikes, enlarged in fruit, peduncle 10 mm. Floral bracts 3–6.5 mm, narrowly ovate, apex acute, sparsely strigose, glabrous margins. Calyx 4.5–7.5 mm, surface sparsely strigose, teeth acute, 1 mm. Corolla 5.5–8 mm, externally glabrous, pale blue or lilac turning white to violet. Superior pair of stamens with vestigial glandular appendages or none, not surpassing thecae, not surpassing corolla mouth; style 1.5–2 mm. Cluses 2–2.5 mm, apex round.

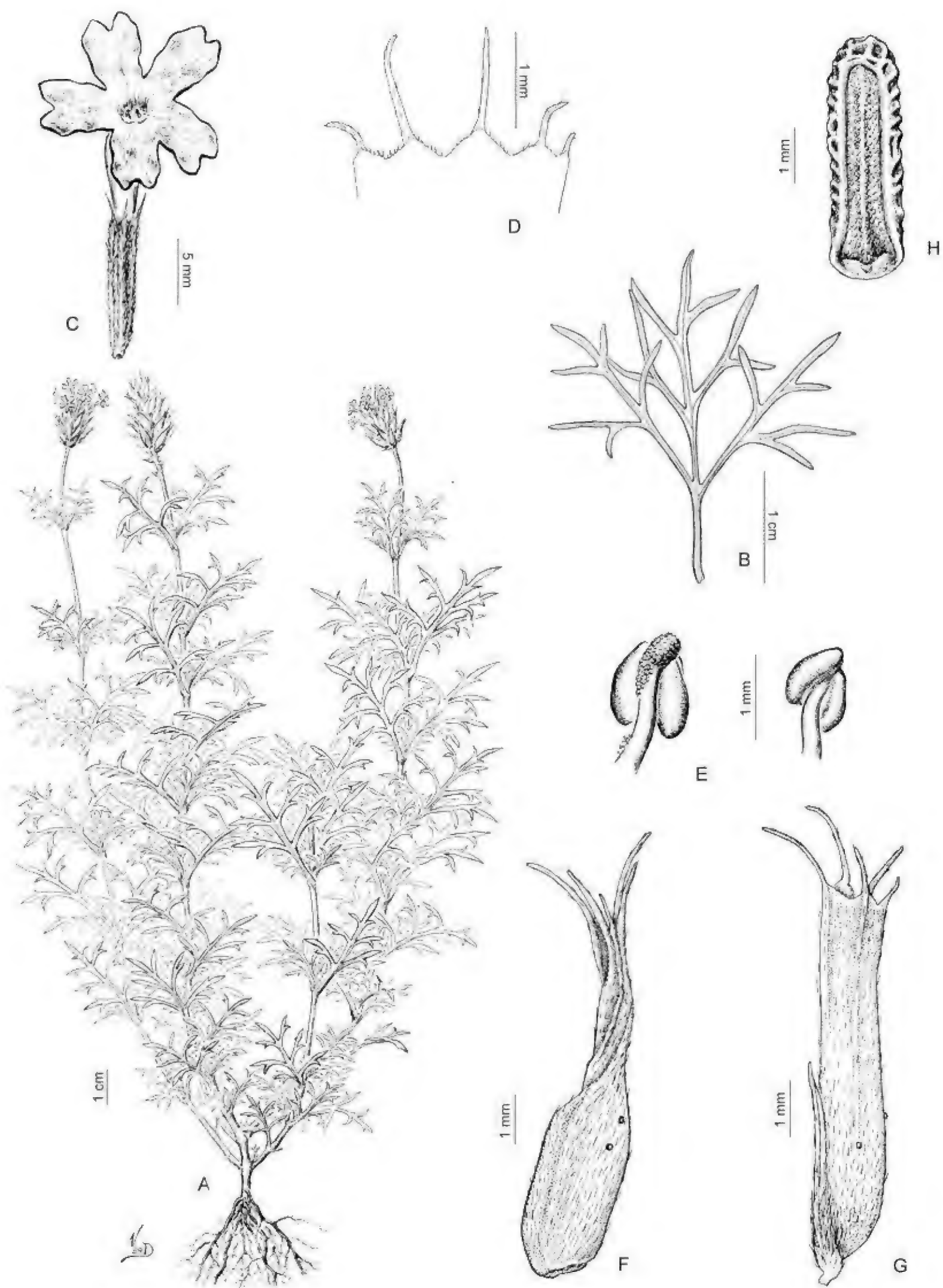


Figure 2. *Glandularia aristigera* (S. Moore) Tronc. —A. Plant, general aspect. —B. Leaf, adaxial surface. —C. Flower. —D. Detail of calyx teeth. —E. Superior pair of stamens. —F. Fructiferous calyx. —G. Calyx and floral bract. —H. Cluse, ventral face. A–H from *Spegazzini s.n.* (LP).

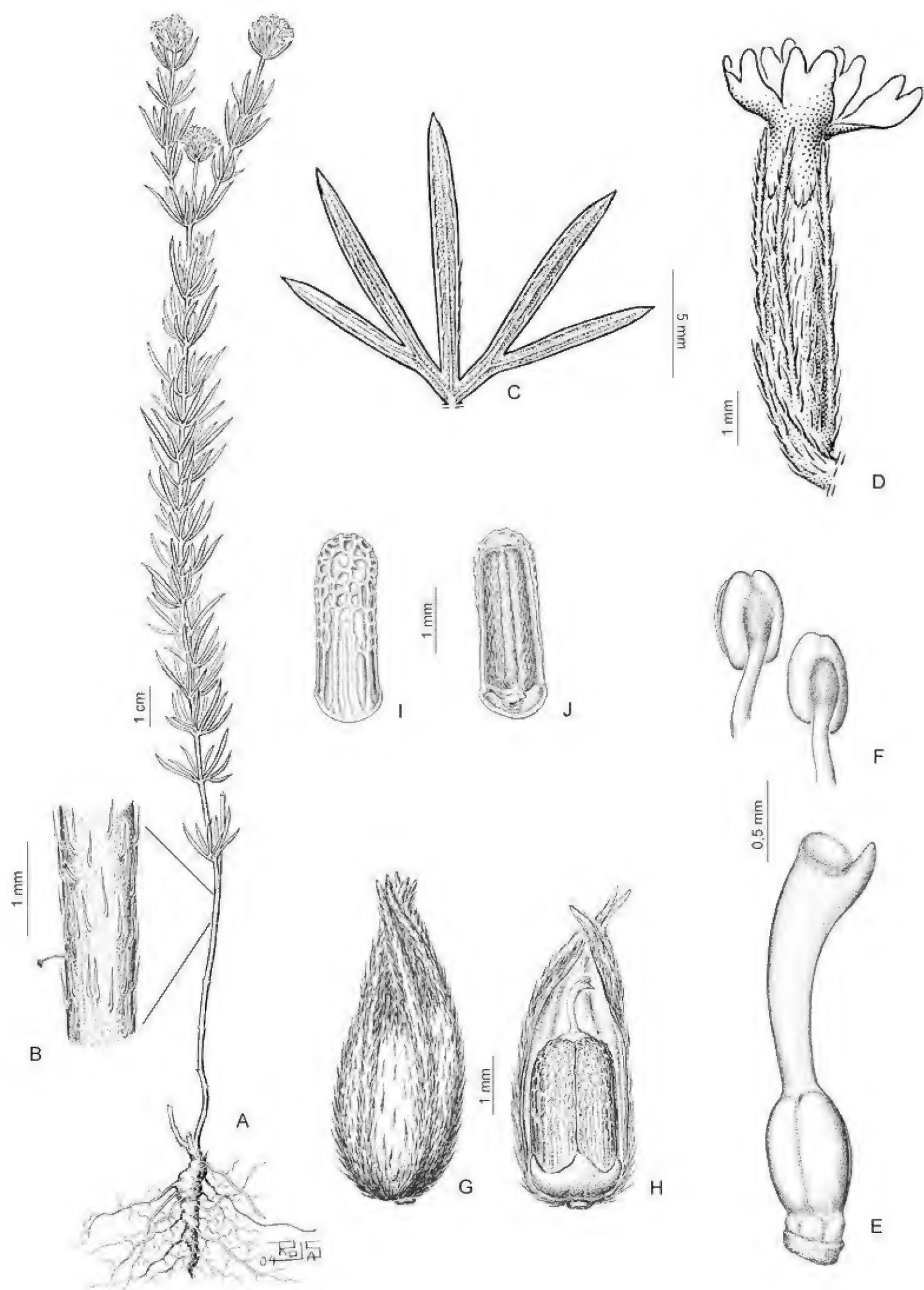


Figure 3. *Glandularia balansae* (Briq.) N. O’Leary. —A. Plant, general aspect. —B. Detail of stem pubescence. —C. Leaf, abaxial surface. —D. Flower with floral bract. —E. Gynoecia. —F. Superior pair of stamens. —G. Fructiferous calyx. —H. Fruit covered by fructiferous calyx. —I. Cluse, dorsal face. —J. Cluse, ventral face. A, C–F from *Rojas* 7537 (SI); B, G–J from *Schinini* 10474 (SI).

Distribution and ecology. *Glandularia balansae* occurs in northeastern Argentina, Brazil, and Paraguay. It inhabits dry fields and grasslands and has also been found in flooded areas.

Notes. *Glandularia balansae* is morphologically similar to *G. thymoides*; see notes under this species.

Selected specimens examined. BRAZIL. **Mato Grosso do Sul:** Ponta Porã, *Hatschbach* 58759 (CTES, SI). **Paraná:** Tibagi, Pilão de Pedra, *Hatschbach* 14658 (MBM, UFPR). **Rio Grande do Sul:** Porto Alegre, Campo da Granja Pinheirinho W de Carazinho, *Ribas* 1689 (MBM). **Santa Catarina:** Laguna, Lagoa Ibiquara, *Forero* 3741 (MBM).

4. *Glandularia catharinae* (Moldenke) N. O’Leary & P. Peralta, *Darwiniana* 45(2): 219. 2007. Basionym: *Verbena catharinae* Moldenke, *Phytologia* 5: 92. 1954. TYPE: Brazil. Santa Catarina: Araranguá, Taimbesinho, 900 m.s.m., 15 Feb. 1946, *P. R. Reitz* 1561 (holotype, HBR!; isotypes, NY [bc] NY000138252!, SI [bc] SI00003796!). Figure 4.

Prostrate herb, stems decumbent with ascending floral branches, pubescence hirsute. Leaves briefly petiolate, petiole 2–4 mm, blade 10–15 × 13–15 mm, 3-parted to 3-dissected, lobes bilobed, apex acute, base attenuate, margin entire and revolute, adaxial surface glabrous with few erect hairs, abaxial surface hirsute-glandular with long patent hairs principally over the nerves. Inflorescences arranged in monobotrya, less frequently in frondose pleiobotrya, lateral paracladia surpassing the terminal florescence, inflorescences represented by dense multifloral spikes, enlarged in fructification, peduncle 30 mm. Floral bracts 3–4 mm, ovate, apex acute, pubescence hirsute, with glandular hairs. Calyx 7–8 mm, the surface hispid with some glandular hairs, teeth triangular, 0.5–1 mm. Corolla 10–15 mm, externally villous, violet, lilac, or pink. Superior pair of stamens with brief glandular appendages, not surpassing thecae, not surpassing corolla mouth, style 10 mm. Cluses 2.5–3 mm, apex round.

Common names. “Camaradinha,” “formosa sem dote,” and “jurupeba.”

Distribution and ecology. *Glandularia catharinae* is endemic to southern Brazil, found in the states of Santa Catarina, Paraná, and Rio Grande do Sul, growing between 500 and 1200 m elevation.

Notes. *Glandularia catharinae* is similar to *G. jordanensis* and *G. hatschbachii*. It is distinguished by its multifloral and showy inflorescences, being paucifloral in *G. jordanensis* and *G. hatschbachii*. In

G. catharinae the corolla is longer (10–15 mm) than in *G. jordanensis* and *G. hatschbachii* (5–6 mm). *Glandularia catharinae* is distinguished from *G. selloi* and from other species that have morphologically similar leaves by the abaxial surface of the leaves being glandular-hirsute with long patent hairs principally over the nerves.

Selected specimens examined. BRAZIL. **Paraná:** Bituruna, Rio Jangada, *Hatschbach* 14968 (MBM, SI, UFPR, UPCB). **Rio Grande do Sul:** Montenegro, Pinhal, *Sehnem* 5052 (PACA, SI). **Santa Catarina:** Água Doce, BR 153, Rio Roseira 18 km S de Horizonte, *Krapovickas* 33668 (CTES, SI).

5. *Glandularia corymbosa* (Ruíz & Pav.) N. O’Leary & P. Peralta, *Darwiniana* 45(2): 219. 2007. Basionym: *Verbena corymbosa* Ruíz & Pav., *Fl. Peruv.* 1, 22, t. 33. 1798, non *Verbena corymbosa* Cham., *Linnaea* 7: 255. 1832. TYPE: Chile. Concepción: s.d., *H. Ruíz & J. Pavon* s.n. (lectotype, designated by O’Leary et al. [2013b: 261], MA [bc] MA00814973!; isoelectotypes, BM [bc] 00544174!, MA [bc] MA00814971!). Figure 5.

Plants suffruticose, 60–100 cm tall, rhizomatous, stems erect, pubescence hispid with glandular hairs. Leaves sessile or briefly petiolate, petiole less than 2 mm, blade 30–60 × 15–30 mm, entire, oblong, apex acute, base truncate or cordate with 2 subamplexicaule lobes, margin serrate-dentate with acuminate irregular teeth, adaxial surface strigose, abaxial surface hispid with prominent nerves. Inflorescences arranged in pleiobotrya with bracteose paracladia, distal paracladia agglutinated in a corymbiform aspect, inflorescences dense multifloral spikes, enlarged in fructification, peduncles 60 mm. Floral bracts 4–7 mm, ovate to linear, apex acute, pubescence hispid, sometimes with some glandular hairs. Calyx 5–7 mm, surface hispid with some glandular hairs, teeth triangular, 1–1.5 mm. Corolla 9–15 mm, externally villous, violet or blue. Superior pair of stamens with vestigial glandular appendages, not surpassing thecae, not surpassing corolla mouth, style 8 mm. Cluses 2.5 mm, apex round.

Common names. “Formosa sem dote.”

Distribution and ecology. *Glandularia corymbosa* has a wide area of distribution; however, it is apparently never frequent. It is found in Chile, Brazil, and Uruguay. It is probably present in Argentina but has never been collected there.

Notes. *Glandularia corymbosa* can be distinguished by its type of inflorescence, not frequent in *Glandularia* species, which is a pleiobotrya with

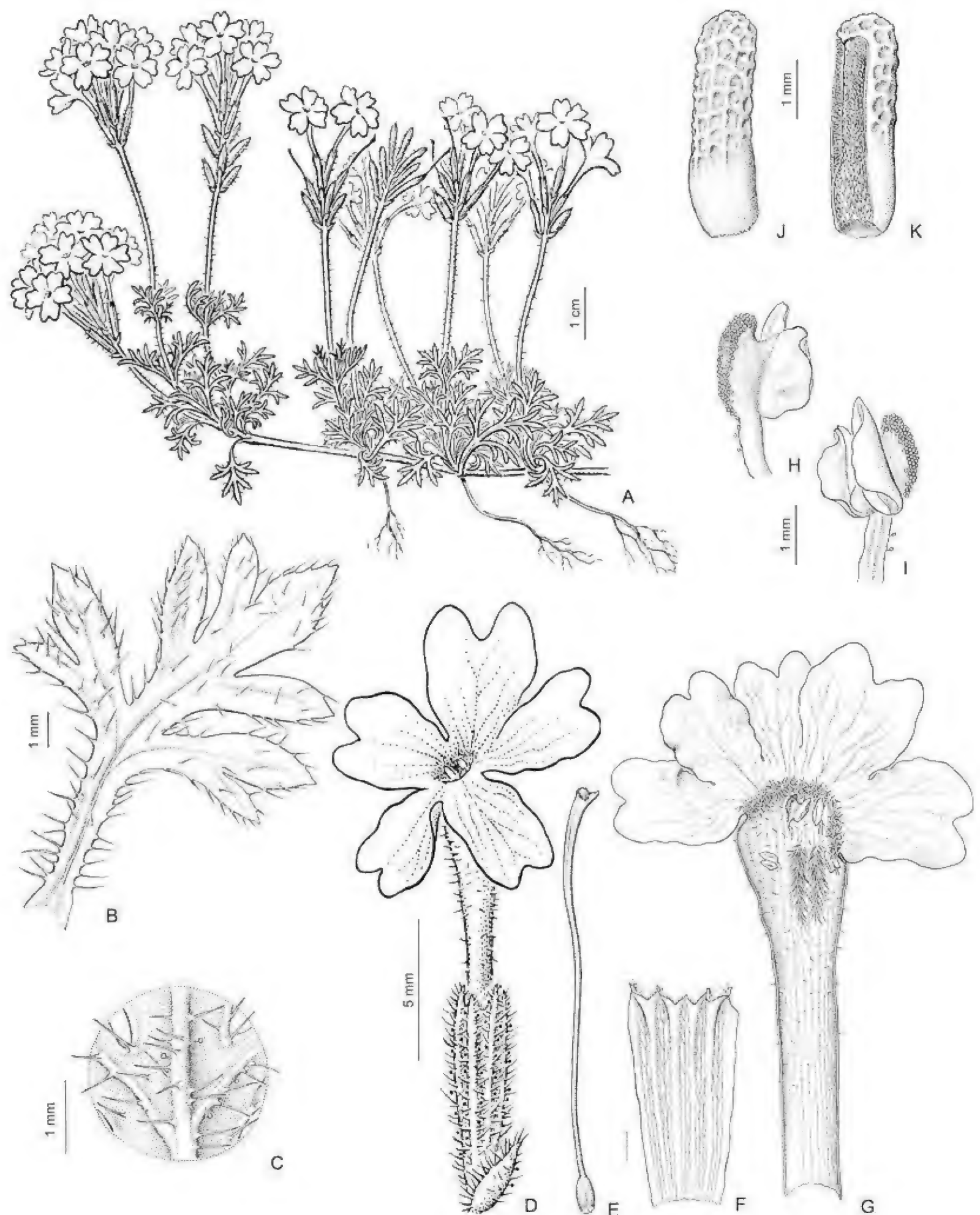


Figure 4. *Glandularia catharinae* (Moldenke) N. O'Leary & P. Peralta. —A. Plant, general aspect. —B. Leaf, adaxial surface. —C. Detail of leaf pubescence, abaxial surface. —D. Flower with floral bract. —E. Gynoecium. —F. Calyx extended, inner surface. —G. Corolla opened with androecium. —H, I. Superior pair of stamens. —J. Cluse, dorsal face. —K. Cluse, ventral face. A–K from *Sehnem* 5052 (SI).

bracteose paracladia, with distal paracladia agglutinated in a corymbiform aspect. It is also distinguished by its truncate or cordate leaf base with two subamplexicaul lobes.

Selected specimens examined. BRAZIL. **Paraná:** Gral. Carneiro, *Hatschbach* 28316 (MBM, SI). **Rio Grande do Sul:** Bom Jesus, faz. B. Velho, *Rambo* 34774 (SI). **Santa Catarina:** Caçador, *Smith & Reitz* 8977 (SI); Lages, Encruzilhada, *Klein* 3200 (SI).

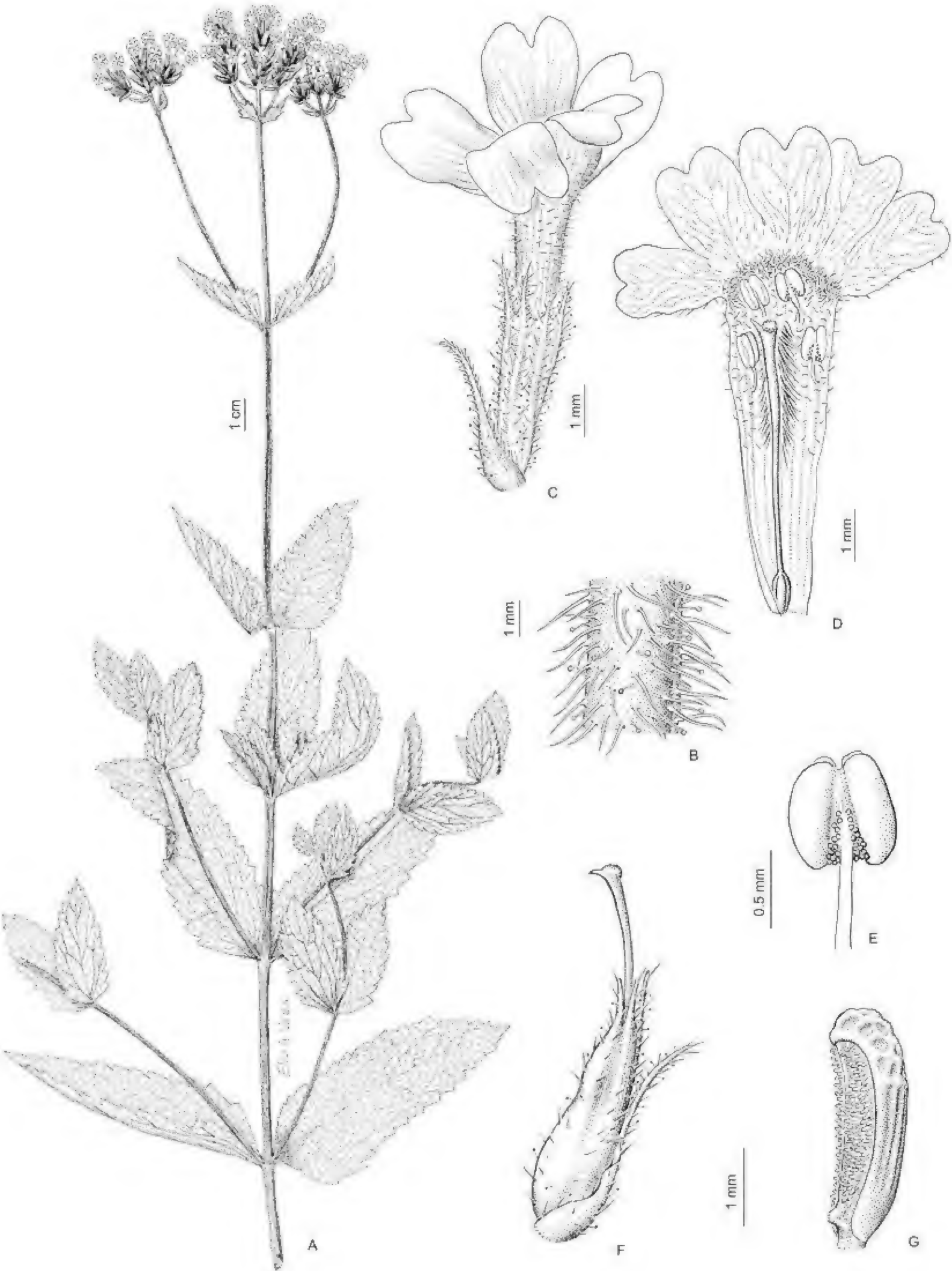


Figure 5. *Glandularia corymbosa* (Ruíz & Pav.) N. O'Leary & P. Peralta. —A. Branch, general aspect. —B. Detail of stem pubescence. —C. Flower with floral bract. —D. Corolla opened with androecia and gynoecia. —E. Superior stamen. —F. Fructiferous calyx. —G. Cluse, lateral face. A from *Smith & Reitz 8977* (SI); B–G from *Klein 3200* (SI).

6. ***Glandularia dusenii*** (Moldenke) N. O'Leary & P. Peralta, *Darwiniana* 45: 222. 2007. Basionym: *Verbena dusenii* Moldenke, *Phytologia* 2: 422. 1948. TYPE: Brazil. Paraná: Pinhaes, 29 Oct. 1908, *P. K. H. Dusén 7108* (holotype, S; isotypes, LD [bc] LD001403038!, NY [bc] NY0138262!, PH [bc] PH00028756!, SI [bc] SI00003817!, US [bc] US000118690!). Figure 6.

Plants suffruticose, prostrate, stems decumbent with ascending floral branches, strigose to glabrous. Leaves briefly petiolate, petiole 3–7 mm, blade 10–35 × 10–35 mm, 3-parted, apex and base acute, margin serrate to biserrate, both surfaces subglabrous to strigose. Inflorescences arranged in pleiobotrya with frondose paracladia, surpassing the principal florescence or not, inflorescences dense multifloral spikes, enlarged in fructification, peduncle 40–60 mm. Floral bracts 4.5–8 mm, widely ovate, apex acute, glabrous with ciliate margin. Calyx 8–10 mm, hispid over the nerves, teeth aristate, 2 mm. Corolla 12–15 mm, externally villous, violet. Superior pair of stamens with sessile glandular appendages, surpassing thecae, not surpassing corolla mouth, style 8–9 mm. Cluses 4–5 mm, apex rostrate.

Distribution. *Glandularia dusenii* is endemic to the Brazilian state of Paraná.

Notes. *Glandularia dusenii* is distinguished by its widely ovate floral bracts, glabrous except at the margins.

Selected specimens examined. BRAZIL. **Paraná:** Guaraituba, Colombo, *Hatschbach 1519* (MBM, SI).

7. ***Glandularia guaibensis*** P. Peralta & V. Thode, *Rodriguésia* 61(suppl.): 30. 2010. TYPE: Brazil. Rio Grande do Sul: Guaíba, faz. São Maximiano, BR 116, Km. 308, 28 Sep. 2007, *V. Thode 31* (holotype, ICN!; isotype, SI!). Figure 7.

Prostrate to erect herb, stems decumbent or erect, pubescence hispid. Leaves briefly petiolate, petiole 2–3 mm, blade 25–70 × 6–18 mm, entire, elliptic or ovate, apex acute, base attenuate, margin serrate toward apex, entire toward base, adaxial surface strigose, abaxial surface hispid. Inflorescences arranged in monobotrya, less frequently in frondose pleiobotrya, lateral paracladia surpassing the terminal florescence, inflorescences represented by dense multifloral spikes, enlarged in fructification, peduncle 30 mm. Floral bracts 6–7 mm, ovate, apex acute, pubescence hispid. Calyx 8–9 mm, hispid principally on the nerves, the rest strigose, teeth brief, triangular, 0.5 mm. Corolla 13–14 mm, externally villous, lilac

or pink. Superior pair of stamens with glandular appendages, pedicellate and surpassing thecae, not surpassing corolla mouth, style 10 mm. Cluses 3–4 mm, apex round.

Distribution and ecology. *Glandularia guaibensis* is endemic to the Brazilian state of Rio Grande do Sul. Its distribution is restricted to the locality of Guaíba, where this species can be found in swamps. The six collections known are from the same locality; the first was collected in 1985.

Notes. *Glandularia guaibensis* is similar to *G. hasslerana* and *G. paulensis*; see notes under these taxa.

Selected specimen examined. BRAZIL: **Rio Grande do Sul:** Guaíba, BR 116, Km. 307, *Matzembacher s.n.* (ICN 63933).

8. ***Glandularia guaranitica*** Tronc., *Darwiniana* 16: 618–621, fig. 3. 1971. *Verbena guaranitica* (Tronc.) Moldenke, *Phytologia* 23: 211. 1972. TYPE: Argentina. Corrientes: Dpto. San Martín, Tres Cerros, 8 Nov. 1936, *A. Burkart 8028* (holotype, SI [bc] SI00003803!; isotype, SI [bc] SI00003804!). Figure 8.

Plants suffruticose, 50–120 cm tall, stems erect, sometimes decumbent, pubescence hispid, sometimes glandular, retrorse hairs. Leaves briefly petiolate, petiole 5–15 mm, blade 30–100 × 9–27 mm, entire, triangular or ovate, apex acute, base cuneate, margin serrate, adaxial surface strigose, abaxial surface hispid, principally over nerves. Inflorescences arranged in pleiobotrya, with 1 or 2 frondose lateral paracladia, surpassing or not terminal florescence, inflorescences represented by dense multifloral spikes, not enlarged in fructification, peduncle 7–25 mm. Floral bracts 1.5–3 mm, ovate, apex acute, pubescence hispid or strigose, margin ciliate. Calyx 8–9 mm, hispid, retrorse hairs, teeth briefly triangular, 1–1.2 mm. Corolla 19–25 mm, externally with glandular hairs at apical part, the rest glabrous, violet. Superior pair of stamens with subsessile glandular appendages, not surpassing thecae, not surpassing corolla mouth, style 20 mm. Cluses 6 mm, apex rostrate.

Distribution and ecology. *Glandularia guaranitica* is found in northeastern Argentina, southern Brazil, and eastern Paraguay. It grows in high areas in forest margins, up to 300 m.

Notes. *Glandularia guaranitica* is similar to *G. phlogiflora* and *G. megapotamica*. The three species have a similar habit, with the stem pubescence

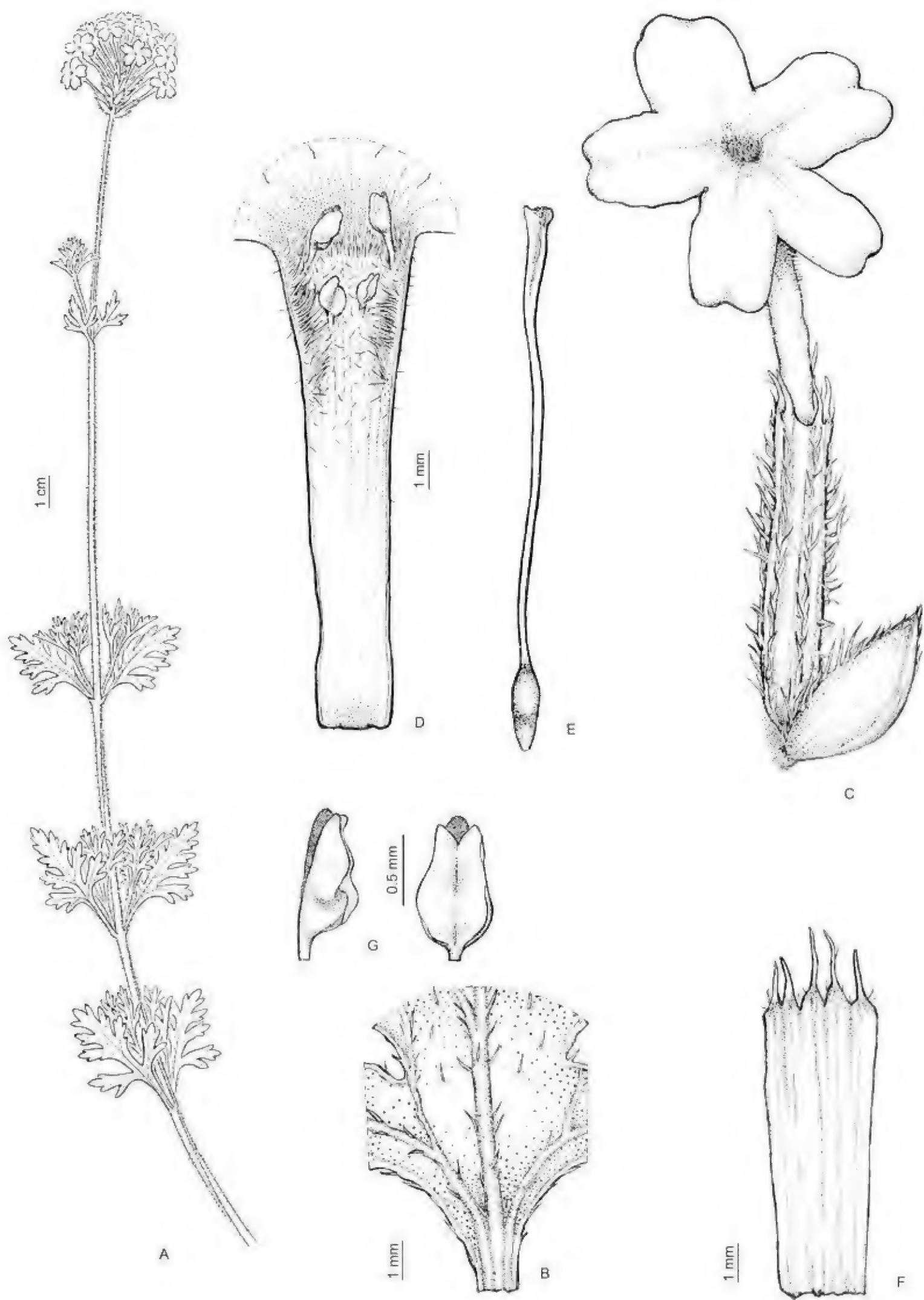


Figure 6. *Glandularia dusenii* (Moldenke) N. O'Leary & P. Peralta. —A. Branch, general aspect. —B. Detail of leaf pubescence, abaxial surface. —C. Flower with floral bract. —D. Corolla opened with androecia. —E. Gynoecia. —F. Calyx extended, inner surface. —G. Superior pair of stamens. A–G from *Hatschbach 1519* (SI).

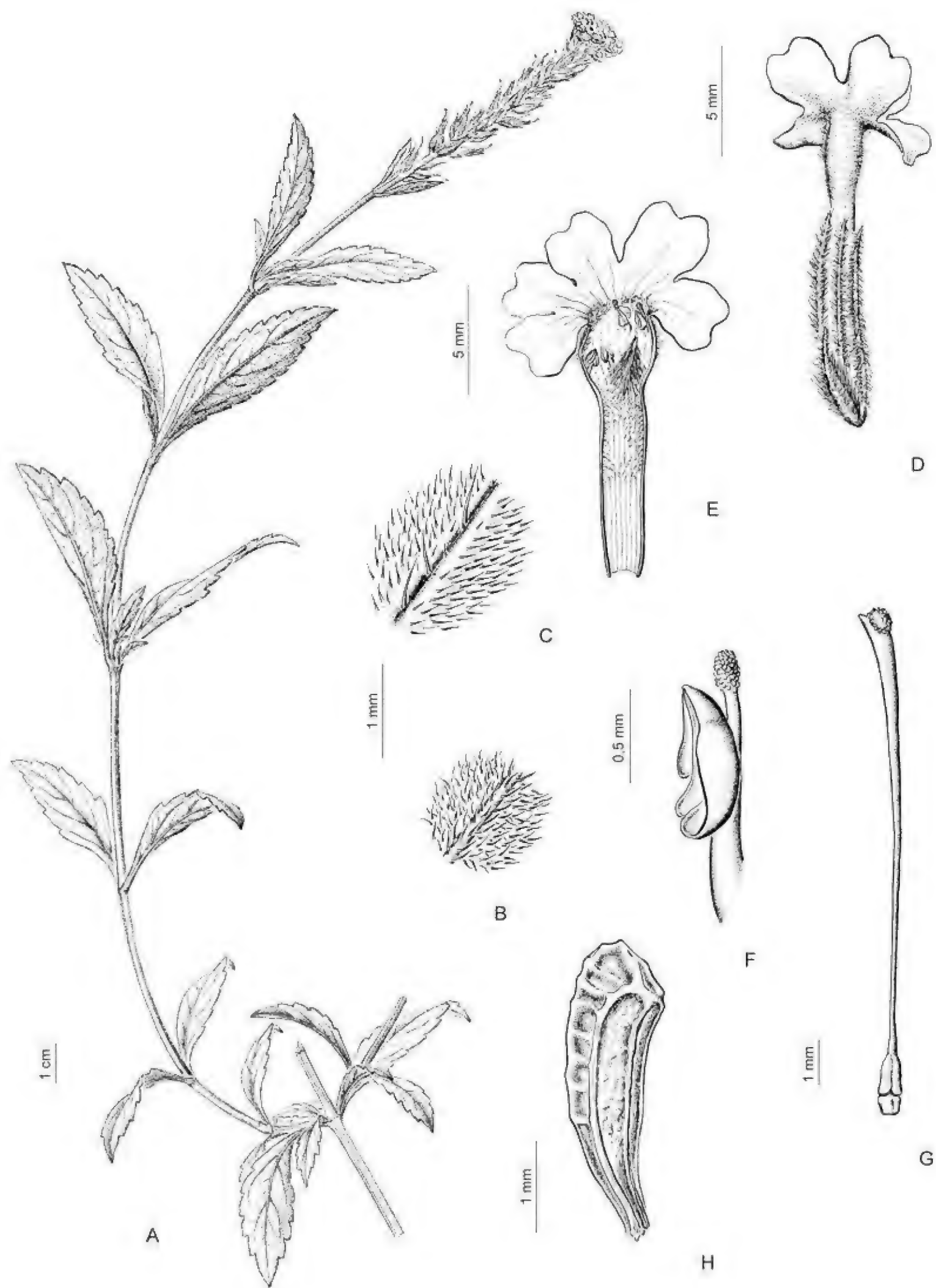


Figure 7. *Glandularia guaibensis* P. Peralta & V. Thode. —A. Branch, general aspect. —B. Detail of leaf pubescence, abaxial surface. —C. Detail of leaf pubescence, adaxial surface. —D. Flower with floral bract. —E. Corolla opened with androecia. —F. Superior stamen. —G. Gynoecia. —H. Cluse, lateral face. A–H from Matzembacher s.n. (ICN).

retorse (especially below the inflorescences), inflorescences not enlarged in fruit, corollas with glandular hairs externally, and the superior pair of stamens with subsessile glandular appendages.

They can be distinguished by the calyx pubescence and teeth shape. In *Glandularia guaranitica* the calyx is hispid with retrorse hairs and it has triangular teeth. In *G. phlogiflora* the calyx is glandular-hirsute with long hispid hairs over the nerves and it has acute teeth. In *G. megapotamica* the calyx is strigose with antrorse hairs and patelliform glands and it has mucronate teeth. Additionally, *G. guaranitica* differs from *G. phlogiflora* in the stem pubescence and shape of the floral bracts. The stem is glandular-hirsute in *G. phlogiflora*, with narrowly ovate floral bracts, 5–6 mm, while in *G. guaranitica* the stem is hispid (sometimes glandular), with ovate floral bracts, 1.5–3 mm. *Glandularia megapotamica* is distinguished by its strigose pubescence on the stems, leaves, and calyx.

Selected specimens examined. BRAZIL. **Rio Grande do Sul:** Pelotas, Morro Redondo, *Pedersen 12592* (CTES, SI). **Santa Catarina:** São Joaquim, banks of Rio Taimbezinho, 1 km E of Bom Jardim da Serra (Cambajuba), *Smith 10203* (SI).

- 9. *Glandularia hasslerana*** (Briq.) Tronc., *Darwiniana* 19: 738. 1975. Basionym: *Verbena hasslerana* Briq., *Bull. Herb. Boissier ser. 2*, 4: 1056. 1904. TYPE: Paraguay. “prope Tobaty in palude,” Sep. [sine anno], *E. Hassler 6464* (lectotype, designated by Peralta & Múlgura [2011: 381], G [bc] G00077157!; isoelectotypes, G [bc] G00077158!, G [bc] G00077156!, MICH [bc] MICH0001108434!, S [bc] S04-2435!, UC [bc] UC000944360!, US [bc] US00000118696!). Figure 9.

Verbena pulchra Moldenke, *Phytologia* 2: 476. 1948. *Glandularia pulchra* (Moldenke) Botta, syn. nov. *Hickenia* 2: 128. 1995. TYPE: Brazil. Paraná: Calmon, 13 Mar. 1910, *K. F. Dusén 9334* (holotype, S [bc] S04-2447!; isotypes, NY [bc] NY000138312!, SI [bc] SI00003918!).

Plants suffruticose, up to 100 cm tall, stems erect, 4-angled, pubescence hispid, retrorse. Leaves petiolate, petiole 8–25 mm, blade 30–150 × 70–35 mm, entire, elliptic to narrowly ovate, apex acute, base attenuate, margin irregularly serrate-crenate, both surfaces strigose. Inflorescences arranged in monobotrya or pleiobotrya with frondose trimerous paracladia, surpassing the principal inflorescence, inflorescences represented by dense multifloral spikes, enlarged in fruit, peduncle 30–150 mm. Floral bracts 5–11 mm, narrowly ovate, apex acute,

strigose or subglabrous with ciliate margin. Calyx 10–14 mm, hispid over nerves, teeth aristate, 2–4 mm. Corolla 18–20 mm, externally villous or with glandular hairs, violet, lilac, or pink. Superior pair of stamens with sessile glandular appendages or none, not surpassing thecae, not surpassing corolla mouth, style 15–17 mm. Cluses 4–5 mm, apex rostrate.

Common names. Flor vovia.

Distribution and ecology. *Glandularia hasslerana* is found in southern Brazil, Paraguay, northeastern Argentina, and Uruguay. It inhabits marshy, sandy, wet, and rocky fields, up to 1000 m.

Notes. *Glandularia hasslerana* shares with *G. guaibensis* and *G. paulensis* the presence of ovate to elliptic leaf blades with serrate, crenate, or dentate margins, an acute apex, and non-glandular pubescence on floral bracts and calyces. *Glandularia hasslerana* is distinguished from *G. guaibensis* and *G. paulensis* by its cluses with rostrate apex and calyx teeth 2–4 mm long. Both *G. guaibensis* and *G. paulensis* have round apex cluses and calyx teeth shorter than 2 mm.

Glandularia hasslerana is similar to *G. nana* in leaf morphology and in having cluses with rostrate apex. *Glandularia nana* is distinguished by having smaller floral bracts (3.5–4 mm vs. 5–11 mm) and hispid-glandular pubescence on floral bracts and calyx.

Glandularia hasslerana is also similar to *G. scrobiculata*; however, the latter is distinguished by its glandular pubescence on the calyx and ovate triangular leaf blades with truncate base.

The study of the type material of *Verbena pulchra*, along with the analysis of several specimens, demonstrates that *V. pulchra* is a synonym of *Glandularia hasslerana*.

Selected specimens examined. BRAZIL. **Rio Grande do Sul:** Gr. Piratini Santo Ângelo, *Hagelund 8139* (SI). **Santa Catarina:** 10 km E de Ponte Serrada, *Krapovickas 33701* (CTES).

- 10. *Glandularia hatschbachii*** (Moldenke) N. O’Leary & P. Peralta, *Darwiniana* 45: 224. 2007. Basionym: *Verbena hatschbachii* Moldenke, *Lloydia* 13: 226. 1950. TYPE: Brazil. Paraná: Piraquara, 13 Nov. 1949, *G. Hatschbach 1621* (holotype, NY [bc] NY00138271!; isotypes, MBM!, SI [bc] SI0003865!). Figure 10.

Prostrate herb, stems decumbent with ascending floral branches, pubescence subglabrous to lightly

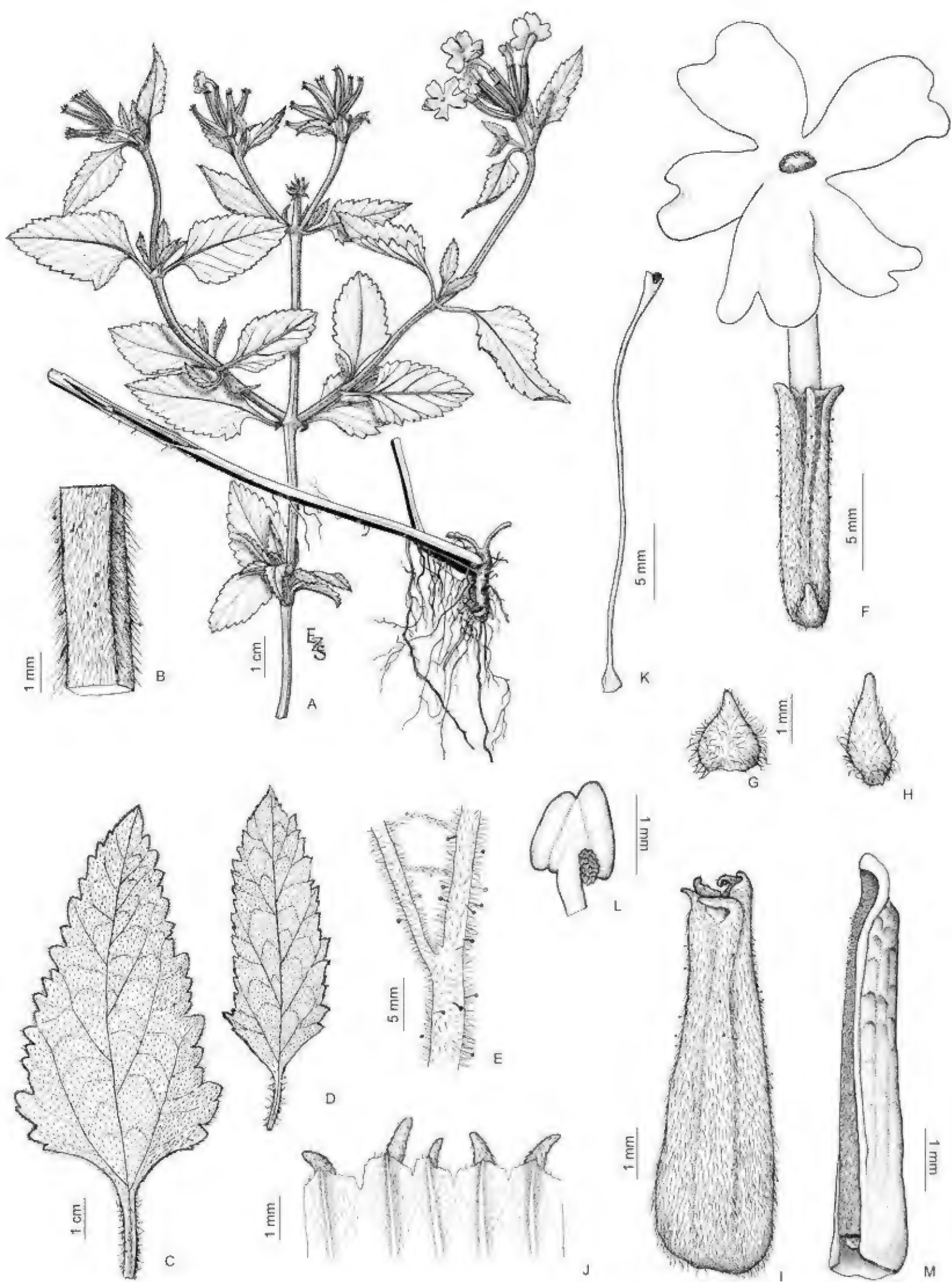


Figure 8. *Glandularia guaranitica* Tronc. —A. Branch, general aspect. —B. Detail of stem pubescence. —C. Basal leaf, adaxial surface. —D. Apical leaf, adaxial surface. —E. Detail of leaf pubescence, abaxial surface. —F. Flower with floral bract. —G, H. Floral bracts. —I. Fructiferous calyx. —J. Calyx extended, apical part, inner surface. —K. Gynoecia. —L. Superior stamen. —M. Cluse, lateral face. A–M from *Burkart 8028* (SI).

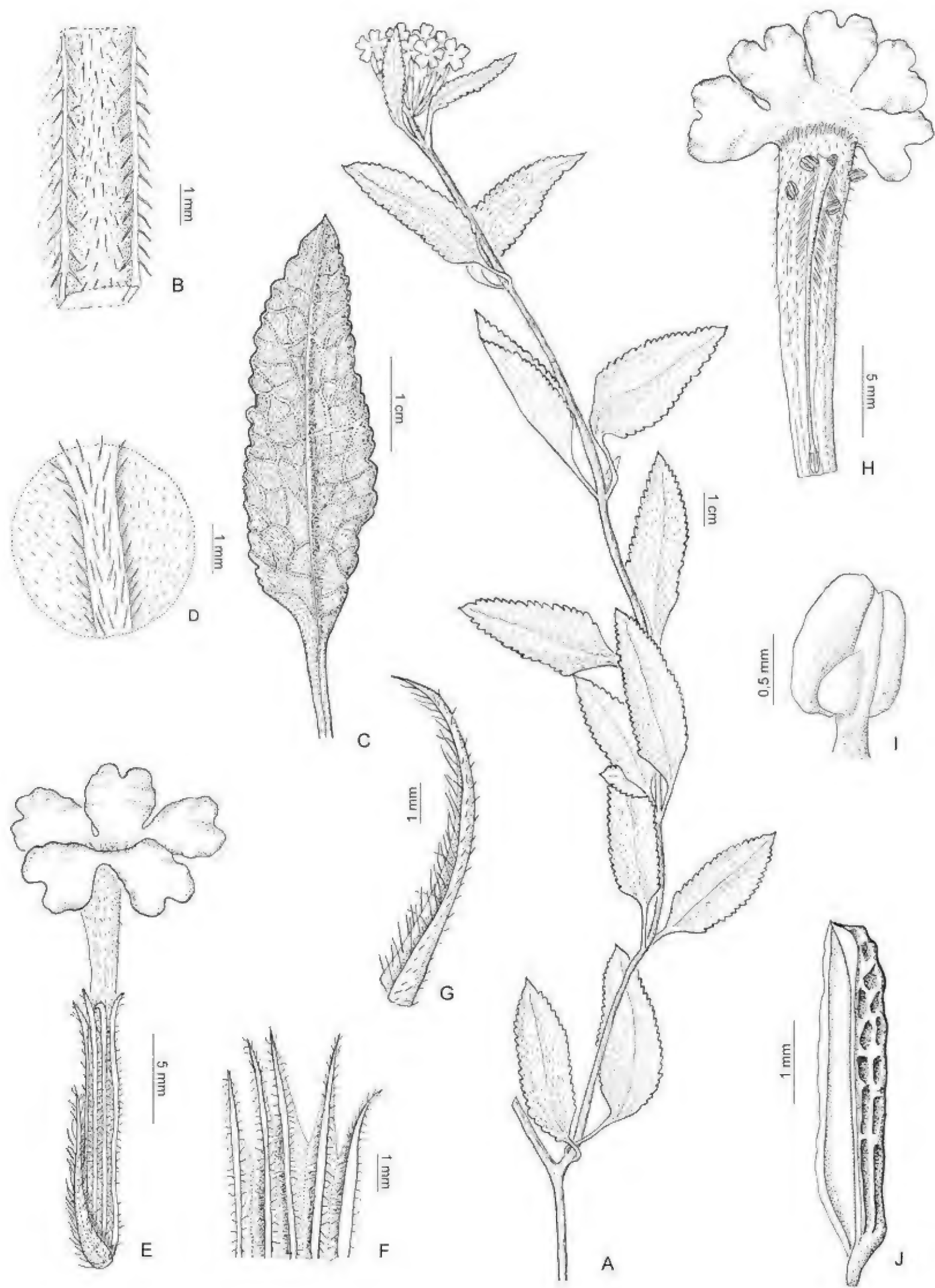


Figure 9. *Glandularia hasslerana* (Briq.) Tronc. —A. Branch, general aspect. —B. Detail of stem pubescence. —C. Leaf, adaxial surface. —D. Detail of leaf pubescence, abaxial surface. —E. Flower with floral bract. —F. Calyx extended, apical part, outer surface. —G. Floral bract. —H. Corolla opened with androecia and gynoecia. —I. Superior stamen. —J. Cluse, lateral face. A–J from *Krapovickas 21608* (SI).

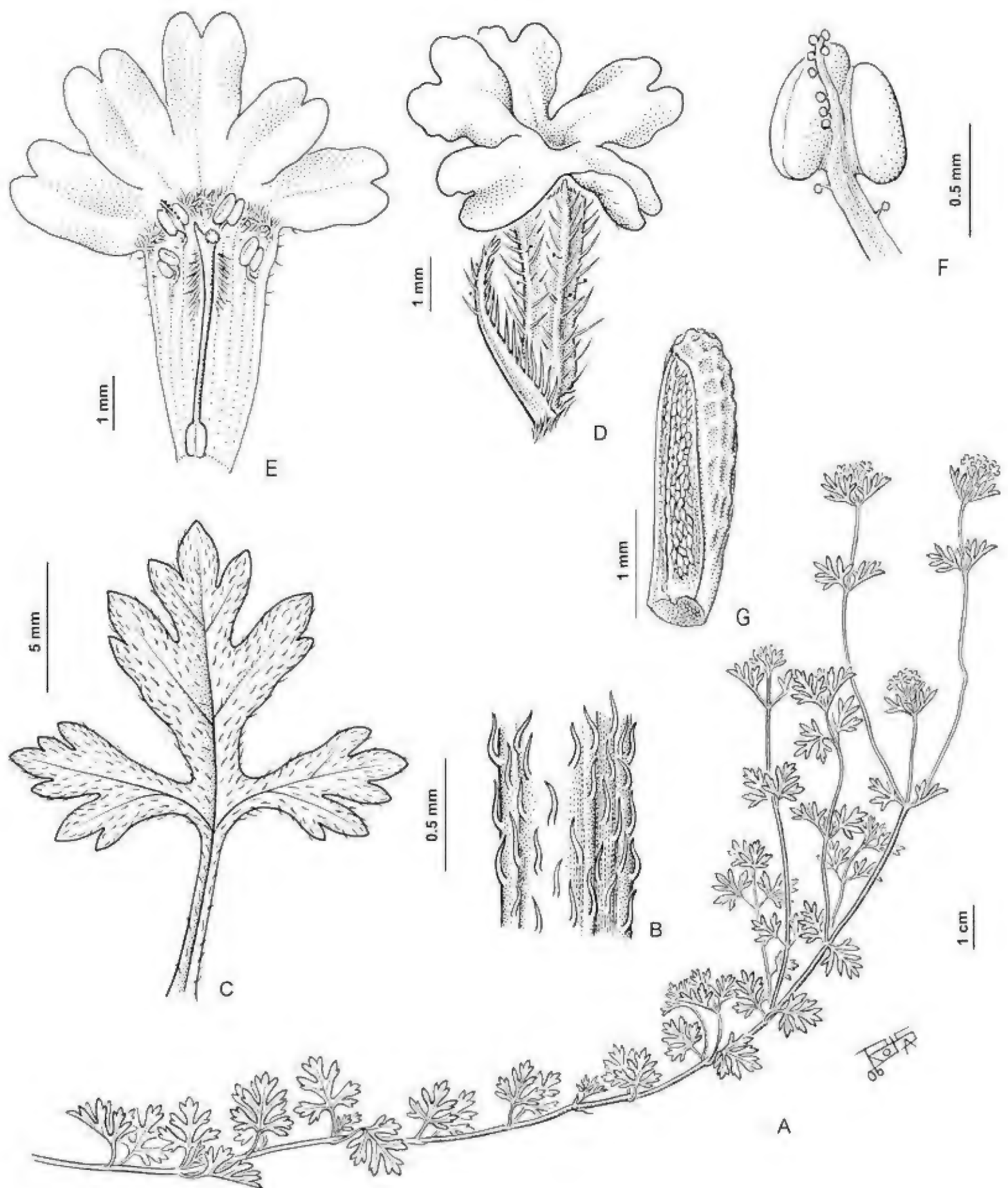


Figure 10. *Glandularia hatschbachii* (Moldenke) N. O'Leary & P. Peralta. —A. Branch general, aspect. —B. Detail of stem pubescence. —C. Leaf, adaxial surface. —D. Flower with floral bract. —E. Corolla opened with androecia and gynoecia. —F. Superior stamen. —G. Cluse, lateral face. A–G from *Smith 7376* (SI).

strigose. Leaves petiolate, petiole 5–10 mm, blade 10–20 × 5–20 mm, 3-parted, segments lobed to parted, apex acute, base truncate to acute, both surfaces strigose. Inflorescences arranged in mono- botrya or pleiobotrya with frondose paracladia, surpassing principal inflorescence, represented by dense paucifloral spikes, umbelliform in anthesis, enlarged in fruit, peduncle 5–20 mm. Floral bracts

4–5 mm, narrowly ovate, apex acute, subglabrous, hispid margin. Calyx 4–5 mm, hispid over nerves, sometimes with some glandular hairs, teeth briefly triangular, 0.5 mm. Corolla 5–6 mm, externally subglabrous, violet or blue. Superior pair of stamens with glandular appendages, surpassing thecae, slightly surpassing corolla mouth, style 4 mm. Cluses 2 mm, apex round.

Distribution and ecology. *Glandularia hatschbachii* is endemic to Brazil, found in the states of Paraná and Santa Catarina.

Notes. *Glandularia hatschbachii* shares with *G. jordanensis* the prostrate habit, non-showy paucifloral inflorescences, short corolla tubes, which are slightly longer than the calyx, and the presence of glandular appendages, slightly surpassing the corolla mouth. *Glandularia hatschbachii* differs in having subglabrous to lightly strigose pubescence and narrowly ovate floral bracts similar in length to the calyx, while *G. jordanensis* has hispid-strigose pubescence and ovate floral bracts shorter than the calyx.

Selected specimens examined. BRAZIL. **Paraná:** São José dos Pinhães, Rio Pequeno, *Hatschbach* 22833 (SI). **Santa Catarina:** Campo Alegre, morro Iquererim, *Smith* 7376 (SI).

11. *Glandularia herteri* (Moldenke) Tronc., *Darwiniana* 19(2–4): 738. 1975. *Verbena herteri* Moldenke, *Revista Sudamer. Bot.* 5: 42–43. 1937. TYPE: Uruguay. Artigas: Santa Rosa Cuareim, 50 m, Nov. 1927, *W. G. Herter* 979 (holotype, NY [bc] NY00138272!; isotypes, B [bc] B10-0247929!, B [bc] B10-02479230!, M [bc] M000111663!, MO [bc] M0000503917!, S [bc] S04-2436!, SI [bc] SI00003789!, U [bc] U0007046!, UC [bc] UC000323326!, US [bc] US0000118698!, WIS [bc] WIS0256126!). Figure 11.

Prostrate herb, stems decumbent, floral branches erect, up to 20–30 cm tall, pubescence subglabrous to lightly strigose. Leaves petiolate, petiole 4–10 mm, blade 8–20 × 7–15 mm, entire, ovate, apex obtuse, base cuneate, margin lobated, both surfaces glabrous. Inflorescences arranged in monobotrya, inflorescences represented by dense multifloral spikes, enlarged in fructification, peduncles 30–100 mm. Floral bracts 4–6 mm, ovate, apex acute, subglabrous, pilose margin. Calyx 6 mm, strigose over nerves, with glandular hairs, teeth acute, 0.5–1 mm. Corolla 11 mm, externally glabrous, violet, lilac, or blue. Superior pair of stamens with glandular appendages, surpassing thecae, slightly surpassing corolla mouth, style 10 mm. Cluses 2–2.5 mm, apex round.

Distribution and ecology. A few collections are known for *Glandularia herteri*, all from northern Uruguay and southern Brazil, in the state of Rio Grande do Sul. It is found in grasslands and moist soils.

Notes. *Glandularia herteri* is distinguished by its subglabrous to lightly strigose pubescence and leaves

with glabrous surfaces, quite different from the other *Glandularia* species.

Selected specimens examined. BRAZIL. **Rio Grande do Sul:** Uruguaiana, rd. from Uruguaiana to Quaraí, by the arroio Garupá, *Pedersen* 12554 (CTES, MBM, SI).

12. *Glandularia humifusa* (Cham.) Botta, *Hickenia* 2: 128. 1995. *Verbena humifusa* Cham., *Linnaea* 7: 271. 1832. TYPE: [Brazil] “*Brazilia meridionales*,” *F. Sellow s.n.* (lectotype, designated here, HAL [bc] HAL00098279!). Figure 12.

Verbena reineckii Moldenke, *Phytologia* 1: 480. 1940. TYPE: Brazil. Rio Grande do Sul: Porto Alegre, Nov. 1897, *J. C. Reineck* 21 (holotype, POM not seen; isotypes, NY not seen, SI image!).

Prostrate herb, stems decumbent, floral branches erect, pubescence lightly hispid. Leaves briefly petiolate, petiole 2–3 mm, blade 15–17 × 9–11 mm, 3-lobed, apex obtuse, base cuneate, margin dentate, both surfaces strigose, principally over nerves. Inflorescences arranged in pleiobotrya with frondose paracladia, surpassing the principal inflorescence or not, inflorescences represented by dense multifloral spikes, enlarged in fruit, peduncles 35–40 mm. Floral bracts 3–3.5 mm, ovate, apex acute, strigose with glandular hairs. Calyx 7.5–8.5 mm, densely hispid mainly over nerves, with glandular hairs, teeth acute, 1 mm. Corolla 12.5–13 mm, externally glabrous, lilac or pink. Superior pair of stamens with vestigial glandular appendages or none, not surpassing thecae, not surpassing corolla mouth, style 10 mm. Cluses 4 mm, apex round.

Distribution and ecology. *Glandularia humifusa* is endemic to Brazil, found only in the state of Rio Grande do Sul.

Notes. *Glandularia humifusa* is distinguished from *G. marruboides* by its floral bracts 3–3.5 mm long and trilobed leaves; the floral bracts are 5.5–6 mm long and leaves are entire in *G. marruboides*.

A suitable lectotype was selected for *Verbena humifusa* among the original material collected by Sellow housed at HAL, with the handwritten note, “*Verbena humifusa* N,” typical of Chamisso’s new species.

Specimen examined. BRAZIL. **Rio Grande do Sul:** Cachoeira do Sul, Durasnal, *Sobral* 2590 (SI).

13. *Glandularia jordanensis* (Moldenke) N. O’Leary & P. Peralta, *Darwiniana* 45: 228. 2007. Basionym: *Verbena jordanensis* Moldenke, *Phytologia* 2: 237. 1947. TYPE: Brazil. São Paulo: Campos do Jordão, Apr. 1945, *J. E. Leite* 3474

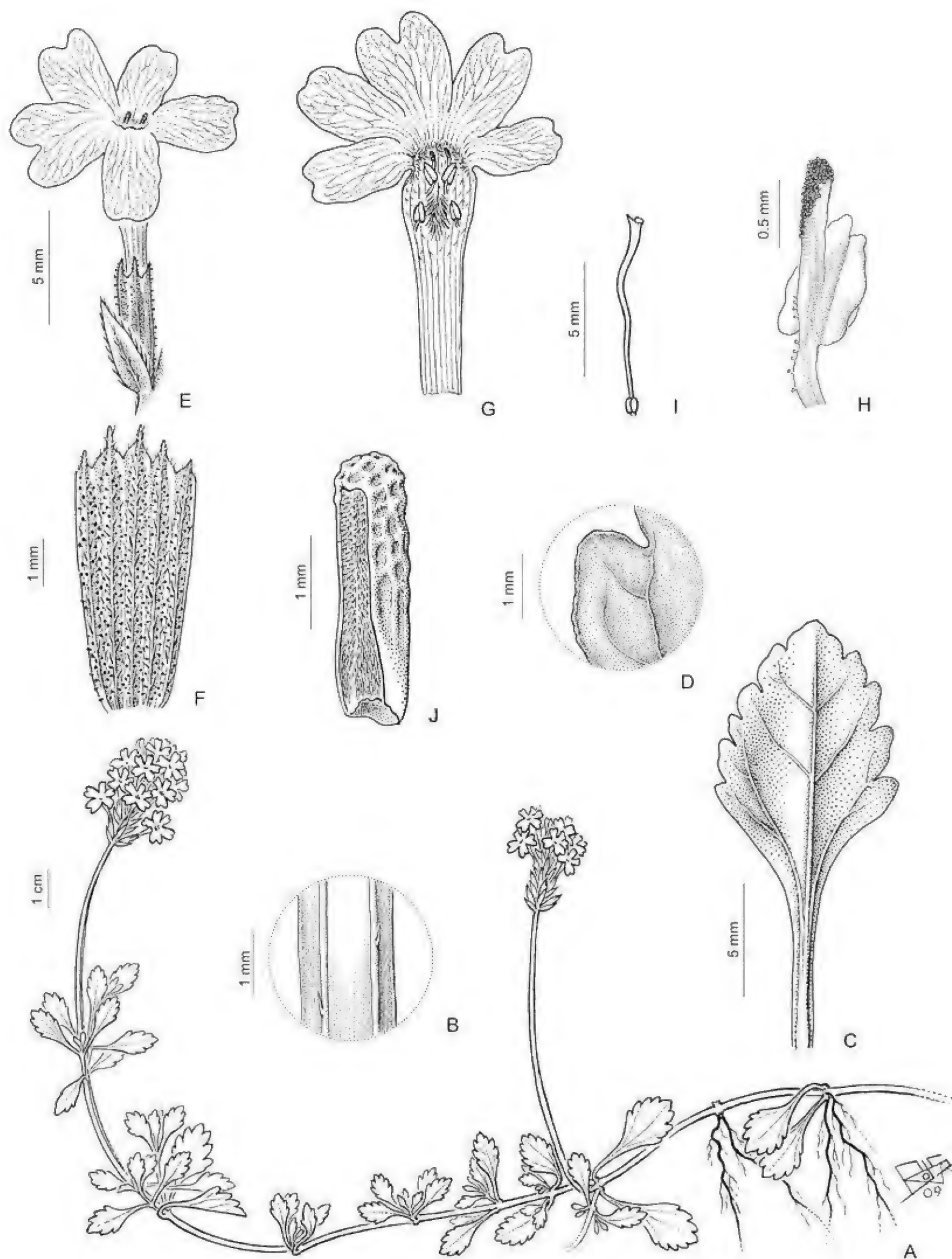


Figure 11. *Glandularia herteri* (Moldenke) Tronc. —A. Branch, general aspect. —B. Detail of stem pubescence. —C. Leaf, adaxial surface. —D. Detail of leaf pubescence, adaxial surface. —E. Flower with floral bract. —F. Calyx extended, outer surface. —G. Corolla opened with androecia. —H. Superior stamen. —I. Gynoecia. —J. Cluse, ventral face. A–J from *Pedersen 12554* (SI).

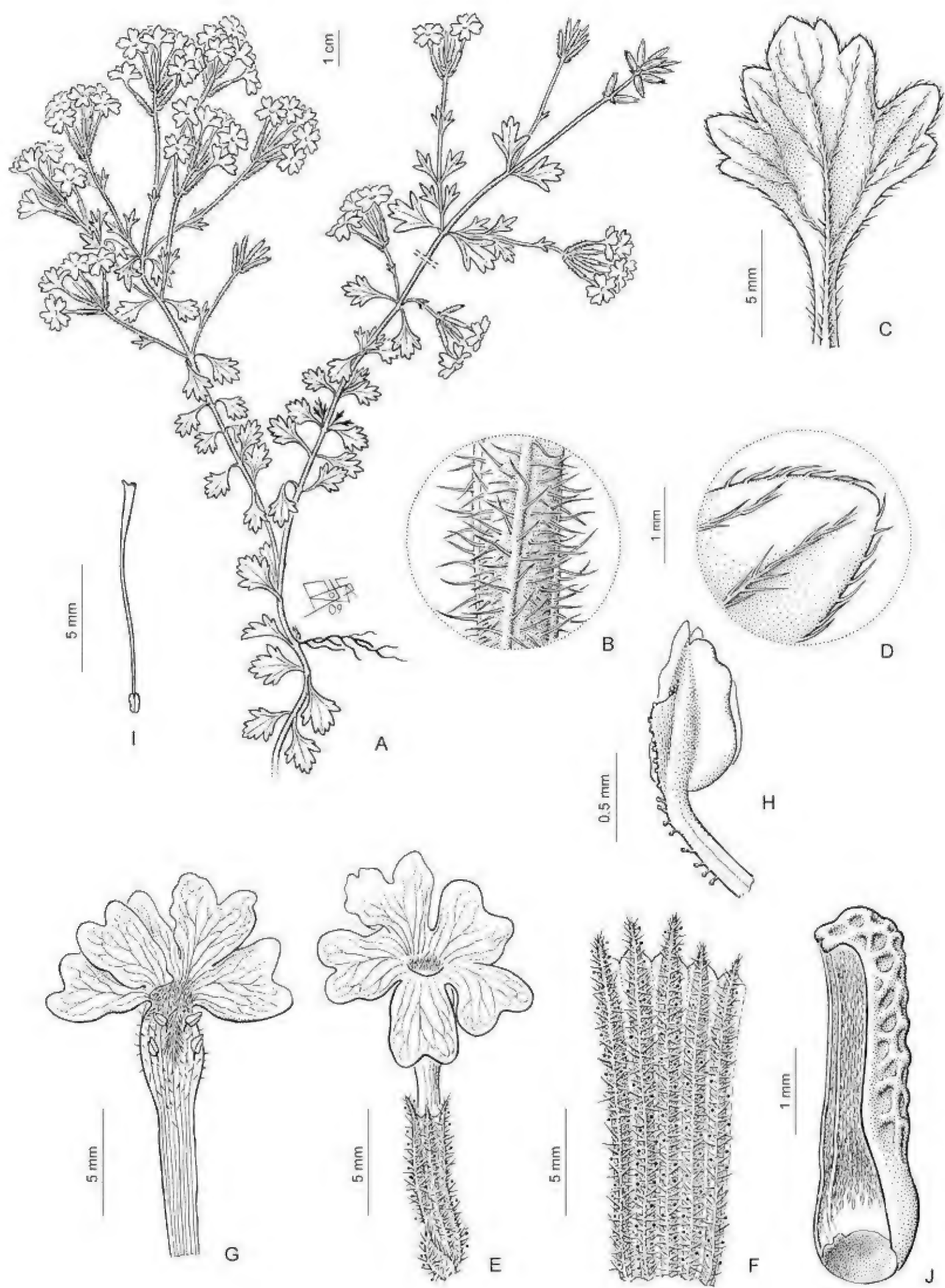


Figure 12. *Glandularia humifusa* (Cham.) Botta. —A. Plant, general aspect. —B. Detail of stem pubescence. —C. Leaf, adaxial surface. —D. Detail of leaf pubescence, adaxial surface. —E. Flower with floral bract. —F. Calyx extended, outer surface. —G. Corolla opened with androecia. —H. Superior stamen. —I. Gynoecia. —J. Cluse, lateral face. A–J from *Sobral* 2590 (SI).

(holotype, FCAB; isotypes, GH [bc] GH00096113!, NY [bc] NY00138279!, SI [bc] SI000003929!). Figure 13.

Verbena campestris Moldenke, Phytologia 3: 117. 1949. TYPE: Brazil. Santa Catarina: Campo dos Padres, 16 Dec. 1948, P. R. Reitz 2392 (holotype, NY [bc] NY000138250!; isotypes, SI [bc] SI00003833!, SI [bc] SI00003834!).

Verbena subpetiolata N. O'Leary, Ann. Missouri Bot. Gard. 94: 613. 2007, replacement name. Replaced synonym: *Verbena lobata* Vell. var. *sessilis* Moldenke, Phytologia 4: 292. 1953, non *Verbena sessilis* (Cham.) Kuntze, Revis. Gen. Pl. 3(2): 257. 1898. TYPE: Brazil. Paraná: S José dos Pinhais, Varzea, 2 Dec. 1952, G. Hatschbach 2876 (holotype, NY [bc] NY000138289!; isotype, SI [bc] SI00003867!).

Prostrate herb, stems decumbent, floral branches erect, up to 20 cm tall, pubescence hispid-strigose, sometimes with glandular hairs. Leaves briefly petiolate, petiole 5 mm, blade 10–20 × 5–20 mm, 3-lobed to 3-parted, apex acute to obtuse, base truncate, margin dentate, adaxial surface strigose, abaxial surface hispid-strigose, principally over the nerves. Inflorescences arranged in monobotrya or pleiobotrya, with frondose lateral paracladia, surpassing terminal inflorescence, inflorescences represented by paucifloral spikes, enlarged in fruit, peduncles 10–30 mm. Floral bracts 3–3.5 mm, ovate, apex acute, pilose margin. Calyx 4–5 mm, hispid over nerves, sometimes with glandular hairs, teeth triangular, 0.5–1 mm. Corolla 5–6 mm, externally villous, violet or blue. Superior pair of stamens with glandular appendages, surpassing thecae, surpassing corolla mouth, style 4 mm. Cluses 2 mm, apex round.

Distribution and ecology. *Glandularia jordanensis* is endemic to southern Brazil, found in the states of Paraná, Santa Catarina, and Rio Grande do Sul. The holotype of this species is from São Paulo; however, it is the only material known from this state. It inhabits grasslands and rocky hills at elevations between 780 and 1800 m.

Notes. *Glandularia jordanensis* is similar to *G. catharinae* and *G. hatschbachii*; see notes under these taxa.

Selected specimens examined. BRAZIL. **Paraná:** Palmas, Sete Butieiros, Hatschbach 30749 (MBM). **Rio Grande do Sul:** Rio Pardo, Palacios 976 (LIL). **Santa Catarina:** São José, Serra da Boa Vista, Reitz 5422 (HBR, SI).

14. *Glandularia lobata* (Vell.) P. Peralta & V. Thode, Rodriguésia 61(suppl.): 30. 2010. *Verbena lobata* Vell., Fl. Flumin. 18: 1825 [1829]; Icon. 1, Tab. 43, 1827 [1831]. TYPE: Vellozo,

1827 [1831]. Icon. 1, tab. 43 (lectotype, designated by O'Leary et al. [2007b: 609]). Figures 14, 15.

Plants suffrutescent, 30–60(–160) cm tall, stems erect or decumbent with ascending floral branches, pubescence variable: hispid, strigose, hirsute or subglabrous, with or without glandular hairs. Leaves petiolate, petiole 5–10 mm, blade 30–60 × 20–40 mm, entire, ovate, triangular, and sometimes trilobed toward base, apex acute, base truncate or round, margin serrate-crenate with acuminate irregular teeth, abaxial surface hispid over nerves. Inflorescences arranged in pleiobotrya with bracteose paracladia with trimerous or tetramerous disposition, inflorescences represented by dense multifloral or paucifloral spikes, enlarged in fruit, peduncles 100 mm. Floral bracts 2–4 mm, ovate, apex acute. Calyx 4–5 mm, hispid with or without glandular hairs, teeth triangular, 0.5–1 mm. Corolla 5–7 mm, externally villous, violet, pink, or blue. Superior pair of stamens with glandular appendages or none, surpassing thecae or not, not surpassing corolla mouth, style 4 mm. Cluses 2 mm, apex round.

KEY TO THE *GLANDULARIA LOBATA* VARIETIES

1. Stems hispid or hirsute, patent hairs up to 3 mm long, floral bract and calyx with glandular hairs; paracladia with tetramerous disposition.....
... *G. lobata* (Vell.) P. Peralta & V. Thode var. *lobata*
- 1'. Stems subglabrous, adpressed hairs shorter than 3 mm long, floral bract and calyx without glandular hairs; paracladia with trimerous disposition *G. lobata* var. *glabrata*
(Moldenke) P. Peralta & V. Thode

14a. *Glandularia lobata* (Vell.) P. Peralta & V. Thode var. **lobata**. Figure 14.

Verbena buchnera Vell., Fl. Flumin. 17: 1825 [1829]; Icon. 1, tab. 42, 1827 [1831]. TYPE: Vellozo, 1827 [1831]. Icon. 1, tab. 42 (lectotype, designated by O'Leary et al. [2007b: 611]).

Verbena lobata Vell. var. *hirsuta* Moldenke, Phytologia 2: 423. 1948. TYPE: Brazil. Rio Grande do Sul: Pinhal prope Santa Maria, 27 Nov. 1902, G. O. A. Malme 1260 (holotype, S; isotype, NY [bc] NY00138288!).

Distribution and ecology. *Glandularia lobata* is known from northeastern Argentina, southern and southeastern Brazil, and eastern Paraguay. It inhabits open fields, forest margins, and wet or rocky fields.

Notes. The presence of paracladia with a tetramerous disposition in *Glandularia lobata* is an exclusive arrangement compared with the rest of the *Glandularia* species.

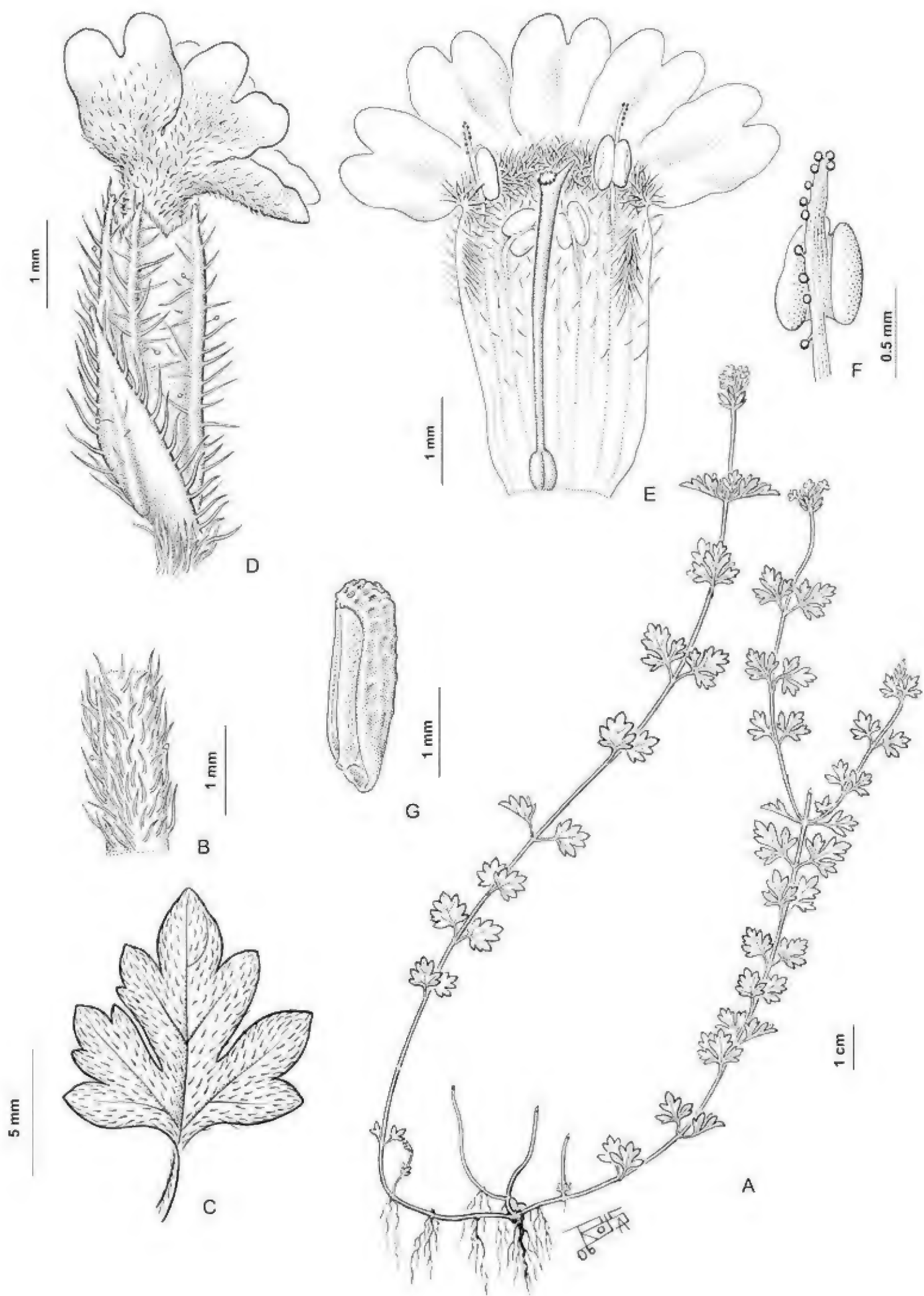


Figure 13. *Glandularia jordanensis* (Moldenke) N. O'Leary & P. Peralta. —A. Plant, general aspect. —B. Detail of stem pubescence. —C. Leaf, adaxial surface. —D. Flower with floral bract. —E. Corolla opened with androecia and gynoecia. —F. Superior stamen. —G. Cluse, lateral face. A–G from Reitz 5422 (SI).

Selected material examined. BRAZIL. **Espírito Santo:** Alegre, Pico da Bandeira, Serra do Caparaó, Irwin 2783 (NY). **Minas Gerais:** Caldas, in ripa anmis Rio Verale, Regnell III1619 (NY). **Paraná:** Curitiba, Barigui, Hatschbach 52324 (SI); São José dos Pinhais, Lagoinha, Hatschbach 2873 (SI). **Rio de Janeiro:** Terezópolis, faz. da Boa Fé, Emygdio 34 (NY). **Rio Grande do Sul:** Giruá, Granja Sodal, Hagelund 4741 (SI). **Santa Catarina:**

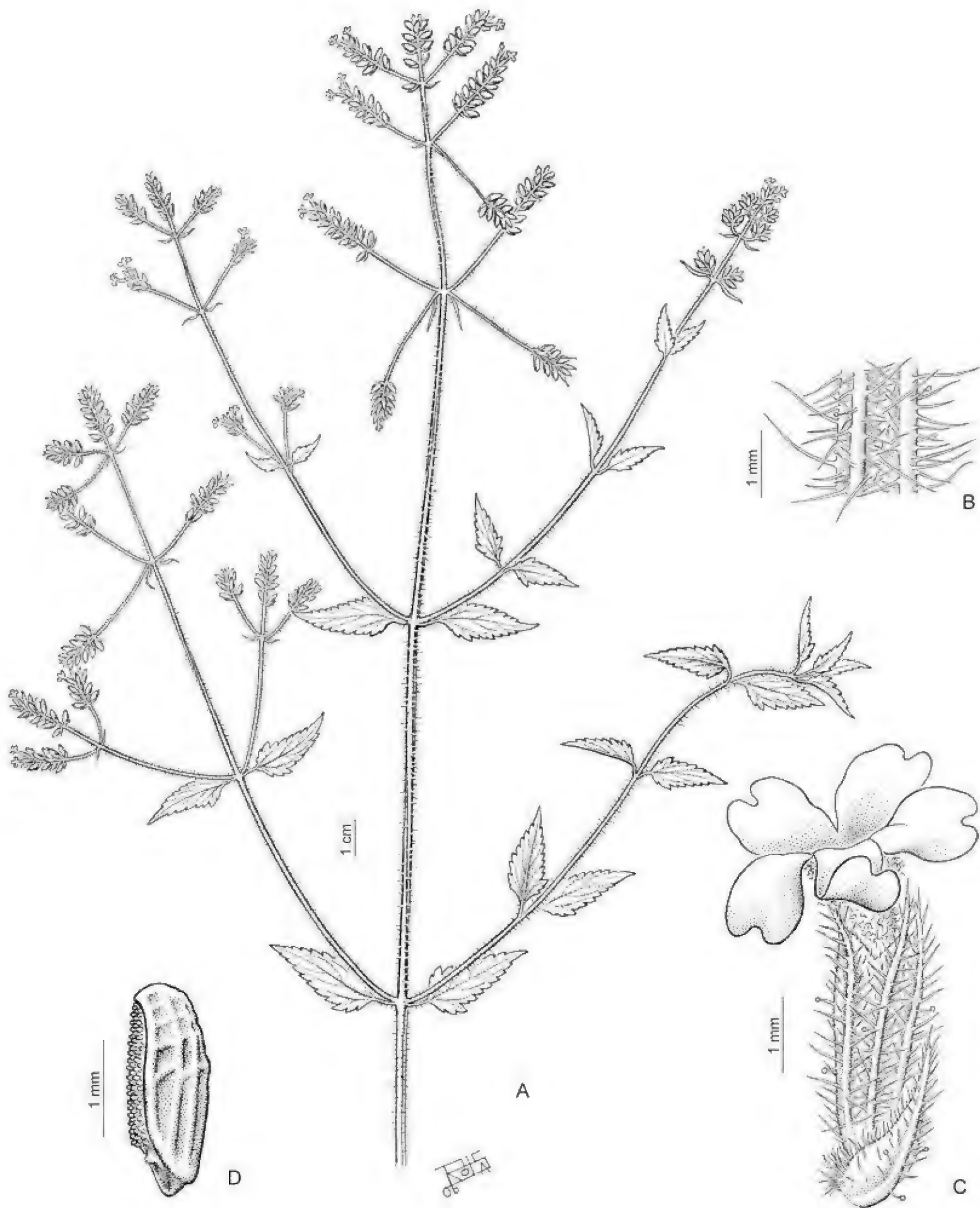


Figure 14. *Glandularia lobata* (Vell.) P. Peralta & V. Thode. —A. Branch, general aspect. —B. Detail of stem pubescence. —C. Flower with floral bract. —D. Cluse, lateral face. A–D from *Hatschbach* 2873 (SI).

Araranguá, Sanga D’Anta, Capoeira, *Reitz c1215* (SI). **São Paulo:** Ubatuba, III. 1940, *A. P. Viégas s.n.* (NY 584709).

14b. *Glandularia lobata* var. *glabrata* (Moldenke) P. Peralta & V. Thode, *Rodriguésia* 61(suppl.): 30. 2010. Basionym: *Verbena lobata* Vell. var.

glabrata Moldenke, *Phytologia* 3: 118. 1949. TYPE: Brazil. Rio Grande do Sul: S Fco. de Paula, 14 June 1937, *B. Rambo 2816* (holotype, NY [bc] NY00138287!; isotypes, LIL [bc] LIL0001375!, LIL [bc] LIL0001376!). Figure 15.

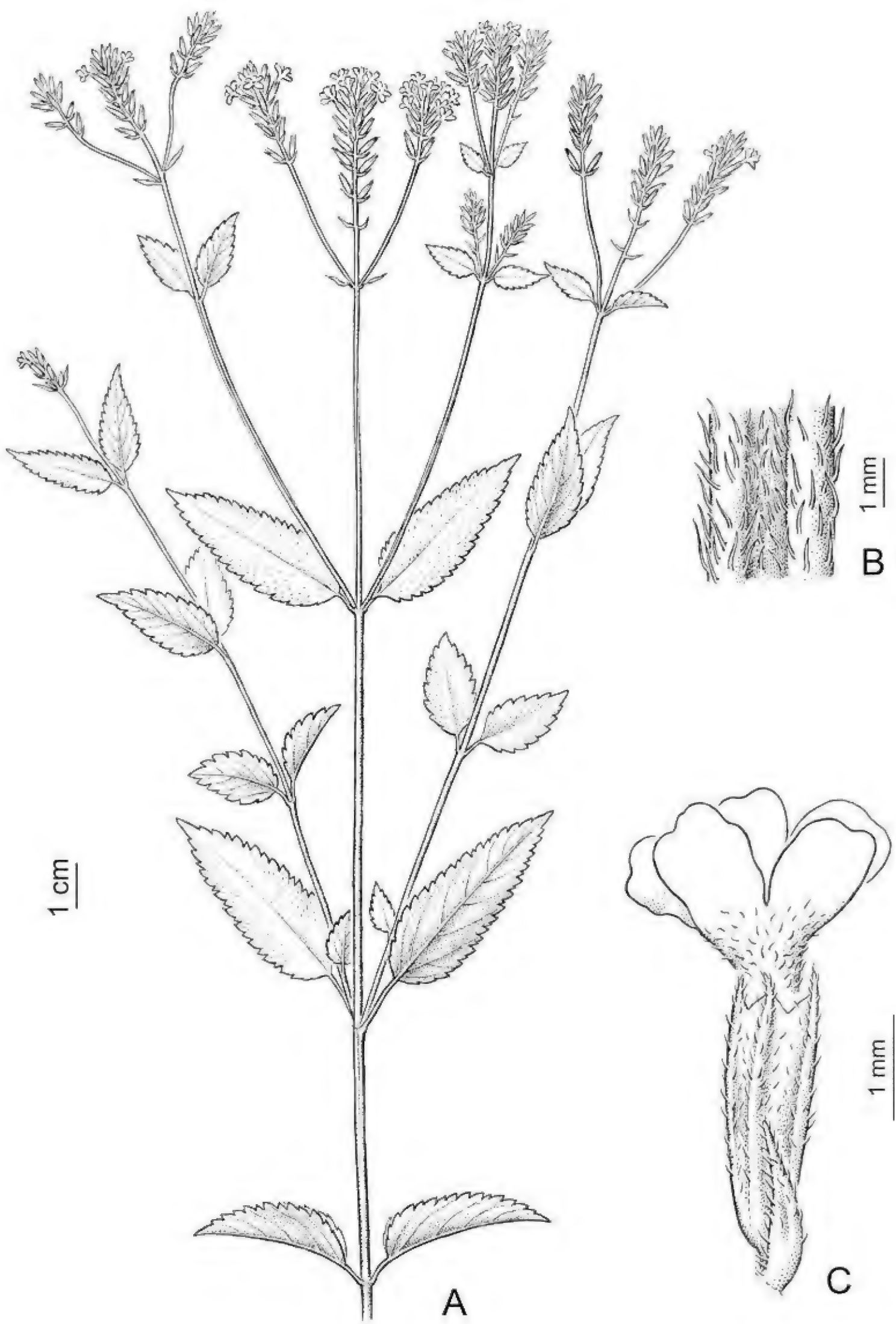


Figure 15. *Glandularia lobata* var. *glabrata* (Moldenke) P. Peralta & V. Thode. —A. Branch, general aspect. —B. Detail of stem pubescence. —C. Flower with floral bract. A–C from *Capell 8* (SI).

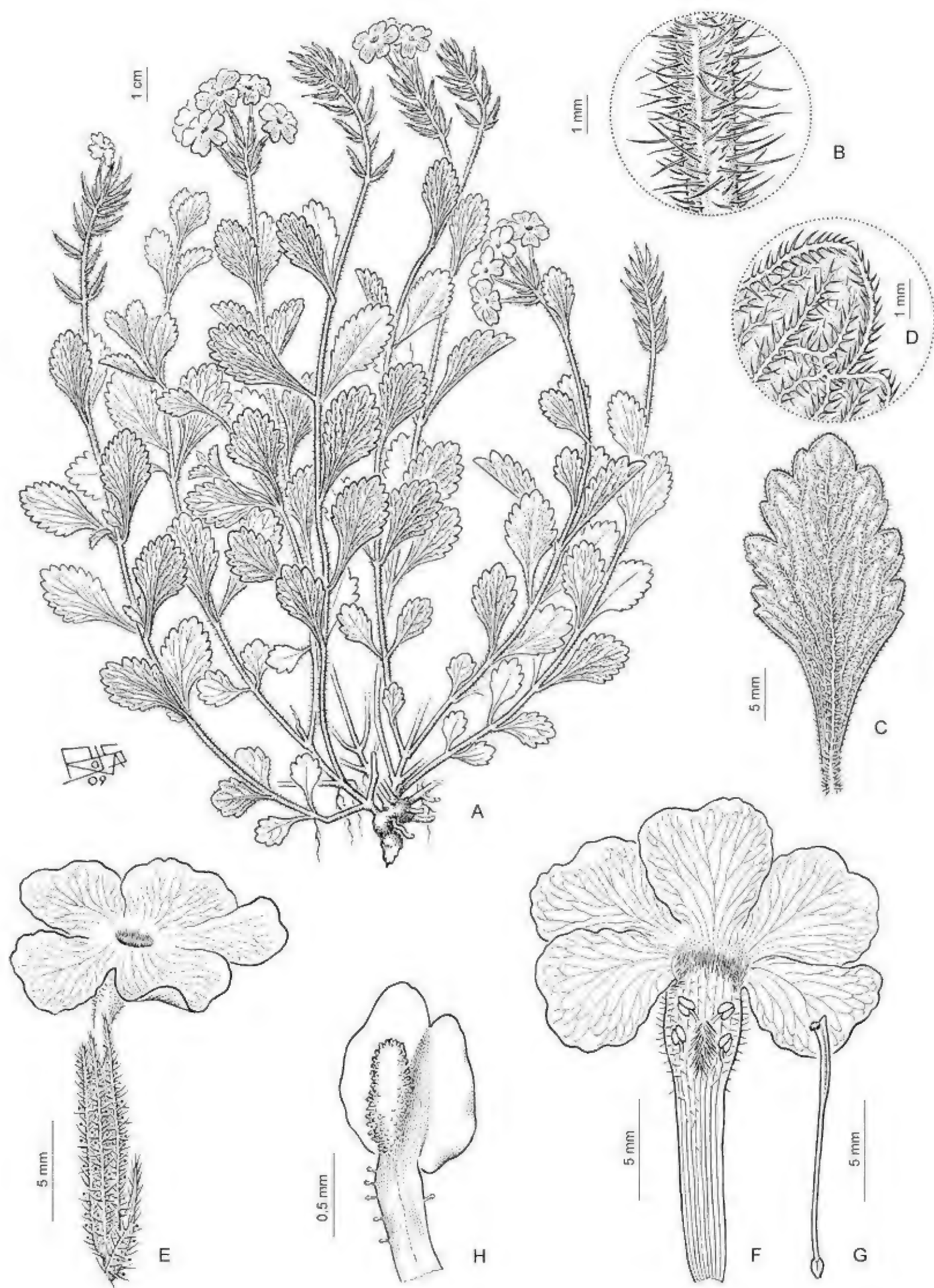


Figure 16. *Glandularia marrubioides* (Cham.) Tronc. —A. Plant, general aspect. —B. Detail of stem pubescence. —C. Leaf, adaxial surface. —D. Detail of leaf pubescence, abaxial surface. —E. Flower with floral bract. —F. Corolla opened with androecia. —G. Gynoecia. —H. Superior stamen. A–H from *Rosengurtt* 9059 (SI).



Figure 17. *Glandularia megapotamica* (Spreng.) Cabrera & G. Dawson. —A, B. Branch general, aspect. —C. Corolla. —D, E. Floral bracts. —F. Calyx and floral bract. —G, H. Superior pair of stamens. —I. Gynoecia. —J. Fructiferous calyx. —K. Cluse, ventral face. —L. Cluse, lateral face. A–L from *Burkart 5127* (SI).

Distribution and ecology. The variety *glabrata* has a more restricted geographical distribution than the typical variety, being found only in southern and southeastern Brazil.

Selected material examined. BRAZIL. **Minas Gerais:** Caparaó, *Porto 1147* (NY). **Paraná:** Morretes, Alto da Serra do Mar (Corvo), 48 km de Curitiba na estrada Curitiba, *Tessmann 3033* (NY). **Rio de Janeiro:** Serra dos Órgãos,

Capell 8 (SI). **Santa Catarina:** Campo Alegre, Morro do Iquererim, *Reitz* 5226 (SI). **São Paulo:** Campos do Jordão, *P. C. Porto* 2984 (NY).

- 15. *Glandularia marruboides*** (Cham.) Tronc., *Darwiniana* 19(2–4): 738. 1975. Basionym: *Verbena marruboides* Cham., *Linnaea* 7: 269. 1832. TYPE: Brazilia meridionalis, s.d., *F. Sellow* (lectotype, designated by O'Leary et al. [2013a: 63], HAL [bc] HAL00098278!, isolecotypes, BR [bc] BR005503926!, K [bc] K000470549!). Figure 16.

Verbena humifusa var. *reticulata* Moldenke, *Phytologia* 2: 423. 1948. TYPE: Brazil. Paraná: in campo into Lago et Desiro Ribas site, 800 m.s.m., 22 Oct. 1914, *P. Dusén* 15714 (holotype, S [bc] S04-2437!; isotypes, F [bc] F0074516!, NY [bc] NY00138274!, US [bc] US000118700!).

Prostrate herb, stems decumbent with ascending floral branches, pubescence glandular-hispid. Leaves sessile, blade 15–25 × 8–15 mm, entire, obovate, apex obtuse, base cuneate, margin dentate, adaxial surface strigose and hispid, abaxial surface hispid with prominent nerves. Inflorescences arranged in monobotrya, less frequently pleiobotrya with frondose paracladia, inflorescences represented by dense multifloral spikes, enlarged in fruit, peduncles 15–45 mm. Floral bracts 5.5–6 mm, narrowly ovate, apex acute, hispid-glandular, ciliate margin. Calyx 8.5–10.5 mm, hispid, with glandular hairs, teeth acute, 2 mm. Corolla 13–15 mm, externally villous, violet or lilac. Superior pair of stamens with vestigial glandular appendages, not surpassing thecae, style 10 mm. Cluses 4 mm, apex round.

Distribution and ecology. *Glandularia marruboides* is endemic to southern Brazil. Moldenke (1964a) mentioned the presence of this species in Argentina and Uruguay; however, it has not been collected there. It grows in rocky, sunny fields, dry fields, and dry riverbeds, at elevations between 50 and 1000 m.

Notes. The abaxial leaf surface of *Glandularia marruboides* has prominent nerves; this is a diagnostic feature. This species is similar to *G. humifusa*; see notes under that species.

Selected material examined. BRAZIL. **Paraná:** Ponta Grossa, Passo de Pupo, *Hatschbach* 17120 (LP, MBM, NY, SI). **Rio Grande do Sul:** Caseiros a Lagoa Vermelha, *Rosengurtt* 9059 (SI). **Santa Catarina:** Lajes, Morro do Pinheiro Seco, *Reitz* 16314 (SI).

- 16. *Glandularia megapotamica*** (Spreng.) Cabrera & G. Dawson, *Revista. Mus. La Plata, Secc. Bot.* 5:

357. 1944. Basionym: *Verbena megapotamica* Spreng., *Syst. Veg.* 4(2): 230–231. 1827. TYPE: Brazil. Rio Grande do Sul: s.d., *F. Sellow* 13 (lectotype, designated by Peralta & Múlgura [2011: 383], K, not seen). Figure 17.

Verbena phlogiflora var. *mucilenta* Schauer, DC. *Prodr.* 11: 538. 1847. TYPE: Brazilia, s.d., *F. Sellow* s.n. (lectotype, designated by Peralta & Múlgura [2011, 383], K [bc] K000470724!; isolecotype, E [bc] E000373264!).

Suffruticose plants, 50–120 cm tall, stems erect, sometimes decumbent, pubescence strigose, retrorse hairs. Leaves briefly petiolate, petiole 10–15 mm, blade 25–70 × 8–12 mm, entire, elliptic to narrowly ovate, apex acute or obtuse, base cuneate, margin serrate, strigose on both surfaces. Inflorescences arranged in pleiobotrya, with 1 or 2 frondose lateral paracladia, surpassing terminal inflorescence, inflorescences represented by dense multifloral spikes, not enlarged in fruit, peduncles 80–100 mm. Floral bracts 3–5 mm, ovate, apex acute, pubescence strigose with patelliform glands, ciliate margin. Calyx 10–12 mm, strigose with patelliform glands, antrorse hairs, teeth mucronate, 0.5 mm. Corolla 13–16 mm, externally with glandular hairs at apical part, the rest glabrous, violet. Superior pair of stamens with subsessile glandular appendages, not surpassing thecae, not surpassing corolla mouth, style 13–15 mm. Cluses 4–4.5 mm, apex rostrate.

Distribution and ecology. *Glandularia megapotamica* grows in northeastern Argentina, southern Brazil, Paraguay, and Uruguay. It has been found in moist soils, grasslands, gallery forests, and forest margins, at lower elevations.

Notes. *Glandularia megapotamica* is similar to *G. guaranitica* and *G. phlogiflora*; see notes under *G. guaranitica*.

Selected material examined. BRAZIL. **Minas Gerais:** Carandaí, *Duarte* 6309 (SI). **Paraná:** Telêmaco Borba, faz. Monte Alegre, *S. I. de Azevedo* 508 (FUEL 41903). **Rio Grande do Sul:** Piratini, *Thode* 122 (ICN). **Santa Catarina:** Bom Jardim da Serra, faz. da Laranja, Bom Jardim, S Joaquim, *Reitz* 7707 (NY).

- 17. *Glandularia nana*** (Moldenke) Tronc., *Darwiniana* 19: 738. 1975. Basionym: *Verbena nana* Moldenke, *Phytologia* 3: 119. 1949. TYPE: Argentina. Formosa: Dpto. Pirané, 23 Oct. 1945, *I. Morel* 117 (holotype, NY [bc] NY000138297!; isotypes, LIL [bc] LIL0001386!, LIL [bc] LIL0001385!, SI [bc] SI00003907!). Figure 18.

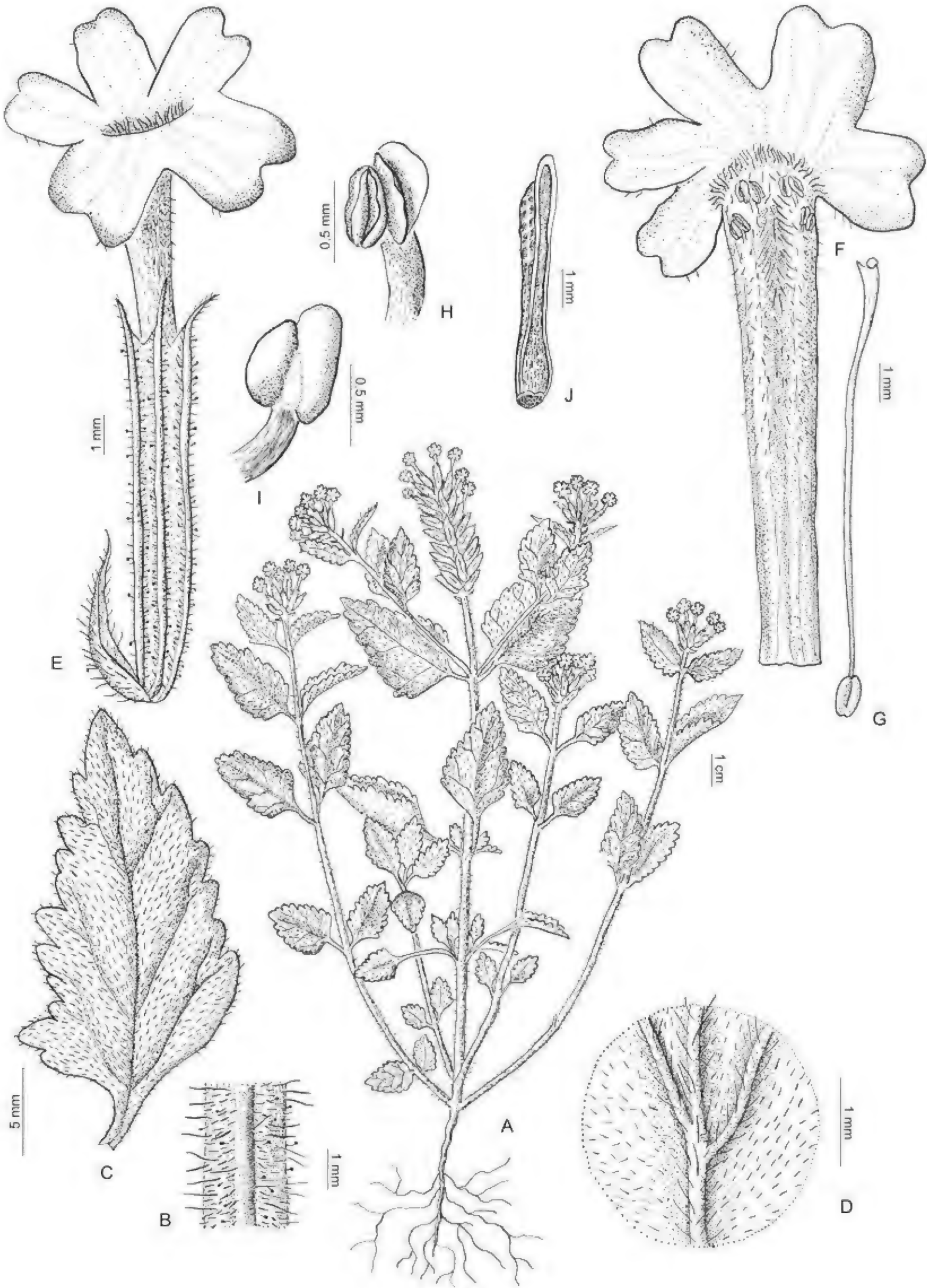


Figure 18. *Glandularia nana* (Moldenke) Tronc. —A. Plant, general aspect. —B. Detail of stem pubescence. —C. Leaf, adaxial surface. —D. Detail of leaf pubescence, abaxial surface. —E. Flower with floral bract. —F. Corolla opened with androecia. —G. Gynoecia. —H, I. Superior pair of stamens. —J. Cluse, ventral face. A–J from Martínez 9693 (SI).

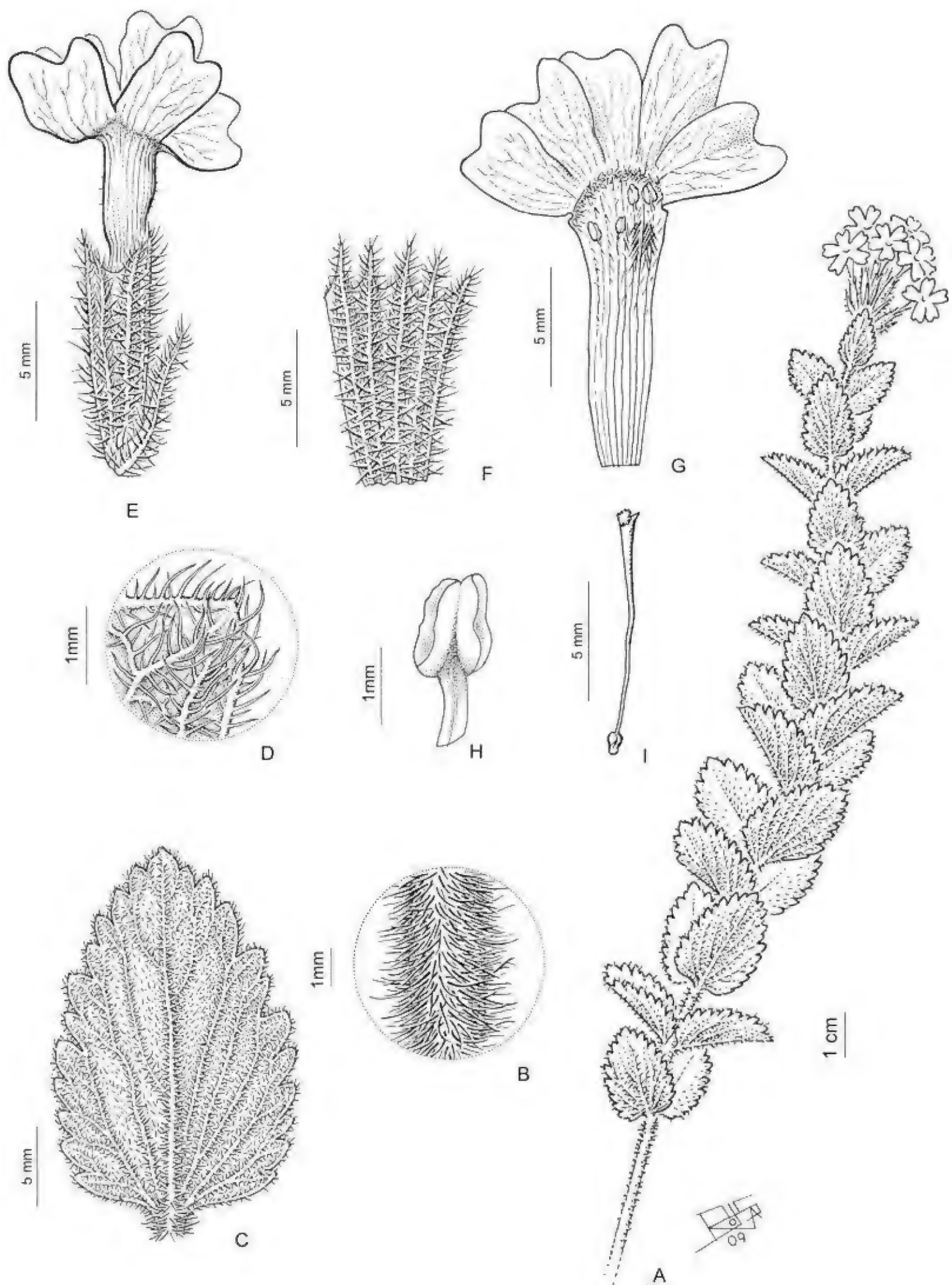


Figure 19. *Glandularia paulensis* (Moldenke) A. L. R. Oliveira & Salimena. —A. Branch, general aspect. —B. Detail of stem pubescence. —C. Leaf, adaxial surface. —D. Detail of leaf pubescence, abaxial surface. —E. Flower with floral bract. —F. Calyx extended, outer surface. —G. Corolla opened with androecia. —H. Superior stamen. —I. Gynoecia. A–I from Souza 5753 (SI).

Verbena pulchra Moldenke var. *paludicola* Moldenke, syn. nov. Phytologia 2: 477. 1948. TYPE: Uruguay. Reanqueras, Rivera, 24/27 Mar. 1907, *G. Herter* 99937 (holotype, NY [bc] NY00138313!).

Verbena hasslerana var. *glandulosa* Moldenke, syn. nov. Phytologia 25: 368. 1973. TYPE: Brazil. Mato Grosso do Sul: Miranda, near rio Miranda, 17 Apr. 1972, *G. Hatschbach* 29600 (holotype, TEX [bc] TEX00375232!).

Prostrate herb or suffrutescent plants, stems erect or decumbent with ascending floral branches, 20–60 cm tall, stems erect, pubescence hirsute-glandular. Leaves petiolate, petiole 8–12 mm, blade 20–40 × 15–20 mm, entire, ovate to triangular, apex acute, base truncate, margin serrate, both surfaces strigose. Inflorescences arranged in monobotrya or pleiobotrya with frondose paracladia, surpassing principal inflorescence or not, inflorescences represented by dense multifloral spikes, enlarged in fruit, peduncle 7–25 mm. Floral bracts 3.5–4 mm, narrowly ovate, apex acute, hispid-glandular. Calyx 9.5–10 mm, hispid-glandular, teeth acute, 1.5–2 mm. Corolla 12–15 mm, externally villous or with glandular hairs, lilac or pink. Superior pair of stamens unappendaged, style 10–12 mm. Cluses 4–6 mm, apex rostrate.

Distribution and ecology. *Glandularia nana* is found in southern Bolivia, northern Argentina, southern Brazil, and Paraguay. It grows in saline clay, wetlands, grasslands, and riparian areas.

Notes. *Glandularia nana* is similar to *G. scrobiculata* by its presence of leaf blades ovate to triangular, with truncate base; however, the former has rostrate apex cluses, while the latter has round apex cluses.

Glandularia nana can also be confused with *G. tomophylla*, with both species having morphologically similar leaves. Nonetheless, *G. tomophylla* can be distinguished by the stamens with glandular appendages, whereas *G. nana* has non-appendaged stamens.

Glandularia nana can be confused with *G. peruviana* and *G. tweediana* because each of those three species has entire leaves and an unappendaged superior pair of stamens. However, *G. peruviana* and *G. tweediana* differ in having round apex cluses.

Glandularia nana is also similar to *G. hasslerana*; see notes under that taxon.

The analyses of the type material of *Verbena pulchra* var. *paludicola* and *V. hasslerana* var. *glandulosa* demonstrated that both are synonyms of *Glandularia nana*.

Selected material examined. BRAZIL. **Mato Grosso do Sul:** Corumbá, faz. Acurizal, Nabileque, Pantanal, *Pott* 3866 (SI). **Rio Grande do Sul:** Quaraí, Serra Javaó,

Pedersen 12556 (SI). **Santa Catarina:** Araranguá, Curralinhos, *Reitz* C. 882 (SI).

18. *Glandularia paulensis* (Moldenke) A. L. R. Oliveira & Salimena, Bol. Bot. Univ. São Paulo 27(2): 149–151. 2009. Basionym: *Verbena paulensis* Moldenke, Phytologia 3: 426. 1951. TYPE: Brazil. São Paulo: Campos do Jordão, Jan. 1944, *E. Frederichs* s.n. (holotype, PACA-27901!; isotypes, NY [bc] NY00138309!, SI!). Figure 19.

Plants suffrutescent, up to 200 cm tall, stems erect, pubescence hirsute. Leaves sessile, blade 15–25 × 12–22 mm, entire, ovate, apex acute or obtuse, base truncate, margin irregularly dentate, pubescence dense hirsute on both surfaces. Inflorescences arranged in monobotrya, inflorescences represented by dense multifloral spikes, enlarged in fruit, peduncles 20–50 mm. Floral bracts 6–8 mm, narrowly ovate, apex acute, pubescence hirsute. Calyx 9 mm, densely hirsute, teeth acute, 1–2 mm. Corolla 10–11 mm, externally villous, violet. Superior pair of stamens unappendaged, style 8 mm. Cluses 3–4 mm, apex round.

Distribution and ecology. *Glandularia paulensis* is endemic to São Paulo, Brazil. It is found mostly in disturbed areas up to 2000 m elevation.

Notes. *Glandularia paulensis* is similar to *G. guaibensis*. These species have different geographical distributions. *Glandularia guaibensis* is endemic to Rio Grande do Sul and *G. paulensis* to São Paulo. Additionally, *G. guaibensis* has calyx teeth that are mucronate to triangular and 0.5 mm long, and a superior pair of stamens with glandular pedicellate appendages, while *G. paulensis* has calyx teeth that are acute, 1–2 mm long, and a superior pair of stamens unappendaged. *Glandularia paulensis* is also similar to *G. hasslerana*; see notes under this species.

Selected material examined. BRAZIL. **São Paulo:** São Bento do Sapucaí, Pedra do Bauzinho, *Souza* 5753 (ESA, SI).

19. *Glandularia peruviana* (L.) Small, Manual S. E. Fl.: 1139. 1933. Basionym: *Erinus peruvianus* L., Sp. Pl. ed. 1, 1: 630. 1753. *Verbena peruviana* (L.) Britton, Ann. New York Acad. Sci. 7: 197. 1893. TYPE: Feuillée, J. Obs. Phys. Math. Bot. [3]: tab. 25, fig. 3. 1725 (lectotype, designated by Moldenke [1964b: 319], tab. 25, fig. 3 in Feuillée, 1725). Figure 20.

Verbena melindres Gillies, Bot. Reg. 14: 1184. 1828. *Verbena chamaedryfolia* Juss. var. *melindres* (Gillies)

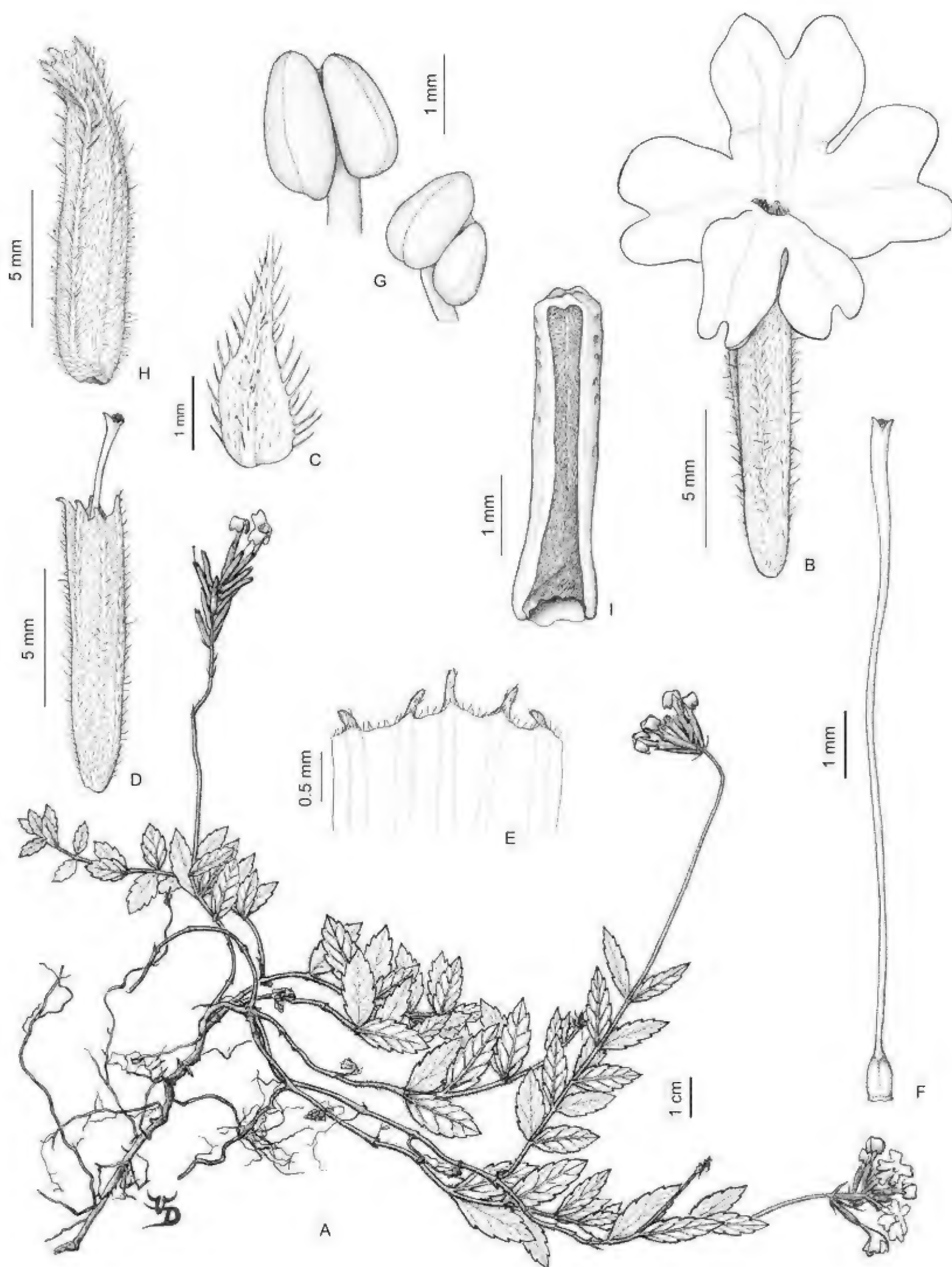


Figure 20. *Glandularia peruviana* (L.) Small. —A. Plant, general aspect. —B. Flower. —C. Floral bract. —D. Calyx. —E. Calyx extended, apical part, inner surface. —F. Gynoecia. —G. Superior pair of stamens. —H. Fructiferous calyx. —I. Cluse, ventral face. A–I from redrawn from Troncoso (1979).

Schauer, Prodr. [DC.] 11: 537. 1847. TYPE: [Argentina.] “Pampas of Buenos Ayres,” *Bot. Reg.* 14: tab. 1184. 1828 (lectotype, designated by Peralta & Múlgura [2011: 387]).

Verbena melindroides Cham., *Linnaea* 7: 270. 1832.
Verbena chamaedryfolia Juss. var. *melindroides* (Cham.) Schauer, Prodr. [DC.] 11: 537. 1847. TYPE: Brazil. Santa Catarina: s. loc., s.d., *F. Sellow s.n.*

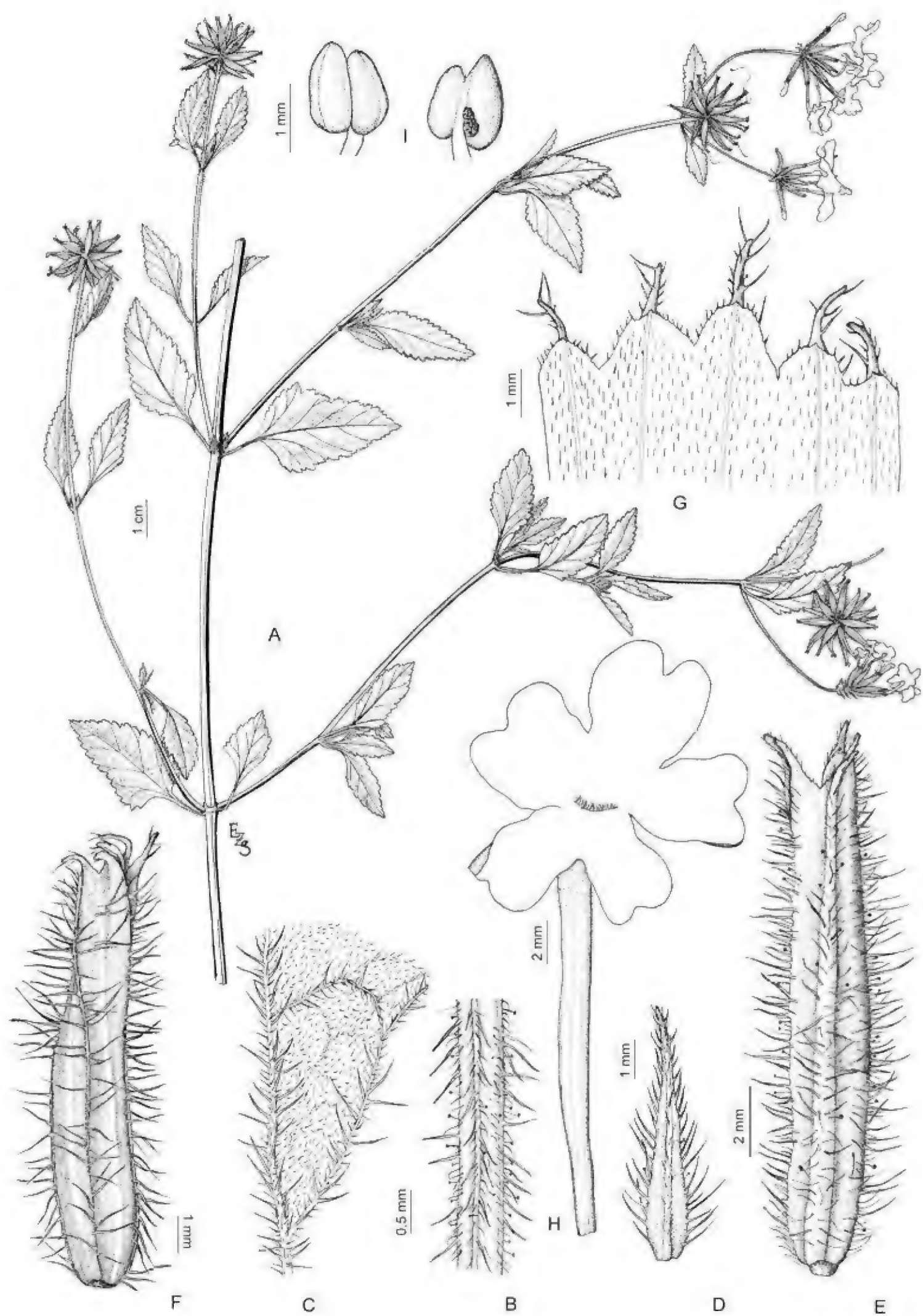


Figure 21. *Glandularia phlogiflora* (Cham.) Schnack & Covas. —A. Branch, general aspect. —B. Detail of stem pubescence. —C. Detail of leaf pubescence, abaxial surface. —D. Floral bract. —E. Calyx. —F. Fructiferous calyx. —G. Calyx extended, apical part, inner surface. —H. Corolla. —I. Superior pair of stamens. A–I from *Klein 4406* (SI).

(lectotype, designated by Peralta & Múlgura [2011: 387], K [bc] K000470559!).

Verbena sanguinea Larrañaga, Escr. Larrañaga 2: 9. 1923. TYPE: *Escritos D. A. Larrañaga 2: 9, Lámina XLII*. 1923 (lectotype, designated by Peralta & Múlgura [2011: 387], tab. XLII in Larrañaga 1923: 9).

Prostrate herb, stems decumbent with ascending floral branches, pubescence hirsute-glandular. Leaves briefly petiolate, petiole 3–8 mm, blade 5–35 × 4–15 mm, entire, ovate to elliptic, apex acute, base cuneate, margin serrate or crenate, adaxial surface strigose, abaxial surface hispid. Inflorescences arranged in monobotrya, inflorescences represented by dense multifloral spikes, enlarged in fructification, peduncle 40–70 mm. Floral bracts 3.5–4.5 mm, ovate, apex acute, pubescence hirsute-glandular. Calyx 9–11 mm, hispid-glandular, teeth triangular, 0.5 mm. Corolla 13–15 mm, externally subglabrous, bright red. Superior pair of stamens unappendaged, style 9–11 mm. Cluses 4–4.5 mm, apex round.

Common name. Camaradinha.

Distribution and ecology. *Glandularia peruviana* is widely distributed in central and northern Argentina, as well as in Bolivia, Brazil, Paraguay, and Uruguay. It grows in rocky outcrops, sand, dry soils, roadsides, grasslands, and wetlands, between sea level and 3000 m.

Notes. *Glandularia peruviana* is similar to *G. tweediana*; the most visible difference is that the first has bright red corollas and the second has lilac or pink, exceptionally white, corollas. This species is also similar to *G. nana*; see notes under the latter.

Selected material examined. BRAZIL. **Rio Grande do Sul:** Santa Maria, faz. Santa Maria, *Moreira Filho* 353 (CTES). **Santa Catarina:** Araranguá, Morro dos Conventos, *Hatschbach* 1993 (CTES).

20. *Glandularia phlogiflora* (Cham.) Schnack & Covas, *Darwiniana* 6(3): 475. 1944. Basionym: *Verbena phlogiflora* Cham., *Linnaea* 7: 266. 1832. *Verbena phlogiflora* Cham. var. *vulgaris* Schauer, *Prodr.* [DC.] 11: 538. 1847. nom. inval. *Verbena megapotamica* Spreng. var. *phlogiflora* (Cham.) Kuntze, *Revist. Gen. Pl.* 3(3): 256. 1898. TYPE: Brazil. s. loc., s.d., *F. Sellow s.n.* (lectotype, designated by Peralta & Múlgura [2011: 390], G!; isoelectotypes, E [bc] E000373265!, K [bc] K000470726!). Figure 21.

Verbena phlogiflora f. *alba* Moldenke, *Phytologia* 4(3): 184. 1953. TYPE: Brazil. Santa Catarina: São Joaquim, in campo Cambajuva, 1200 m.s.m., 23–29 Jan. 1950, *P.*

R. Reitz 3443 (holotype, NY [bc] NY000138310!; isotypes, S [bc] 04-2446!, SI [bc] SI00003802!).

Verbena hasslerana Briq. var. *ovatifolia* Moldenke, *Phytologia* 6(6): 330. 1958. TYPE: Brazil. Santa Catarina: Rio Negrinho, Ruderal Rio Negrinho, 8 Dec. 1956, *L. B. Smith* 8478 (holotype, LL [bc] LL000375233!; isotypes, R [bc] R00196514! US [bc] US000118697!).

Suffruticose plants, 40–70 cm tall, stems erect, sometimes decumbent, pubescence hirsute-glandular, retrorse hairs. Leaves petiolate, petiole 10–20 mm, blade 20–70 × 7–25 mm, entire, ovate, apex acute, base cuneate or truncate, margin irregularly serrate toward apex, adaxial surface strigose, abaxial surface hispid. Inflorescences arranged in monobotrya or pleiobotrya, with 1 or 2 frondose lateral paracladia, surpassing terminal inflorescence, inflorescences represented by dense multifloral spikes, not enlarged in fructification, peduncles 20–50 mm. Floral bracts 5–6 mm, narrowly ovate, apex acute, pubescence hirsute-glandular. Calyx 12–16 mm, hirsute-glandular over nerves, with long hispid hairs, teeth acute, 1–2 mm. Corolla 18–20 mm, externally with glandular hairs only at apical part, violet. Superior pair of stamens with vestigial, subsessile glandular appendages, not surpassing thecae, not surpassing corolla mouth, style 17–18 mm. Cluses 5–5.5 mm, apex rostrate.

Common name. Canaradinha.

Distribution and ecology. *Glandularia phlogiflora* grows in eastern Argentina, southern Brazil, and Paraguay. It is found in moist soils, swamps, forests margin, roadsides, at elevations between 200 and 1200 m.

Notes. *Glandularia phlogiflora* is similar to *G. guaranitica* and *G. megapotamica*; see notes under *G. guaranitica*.

Selected material examined. BRAZIL. **Mato Grosso do Sul:** Rio Brilhantes, faz. Bela Vista, *Hatschbach* 26081 (SI). **Minas Gerais:** Belo Horizonte, *H. L. M. Barreto* 11583 (BHCB 1846). **Paraná:** Bituruna, Rio Jangada, *Hatschbach* 14967 (SI). **Rio de Janeiro:** Parque Nacional do Itatiaia, *P. Occhioni* 9200 (MBM 73817). **Rio Grande do Sul:** Porto Alegre, Morro da Polícia, *Rambo* 37693 (SI), Lajes, Paso do Socorro, *Klein* 4406 (SI). **Santa Catarina:** Riqueza, rocky banks & stream bed, Rio Iracena, E of riqueza, *Smith* 12592 (LP). **São Paulo:** Campos do Jordão, *M. J. Robim et al.* 718 (SP).

21. *Glandularia platensis* (Spreng.) Schnack & Covas, *Darwiniana* 6(3): 475. 1944. *Verbena platensis* Spreng., *Syst. Veg.* 2: 748. 1825. TYPE: Brazil. s. loc., s.d., *F. Sellow s.n.* (neotype, designated by Peralta & Múlgura

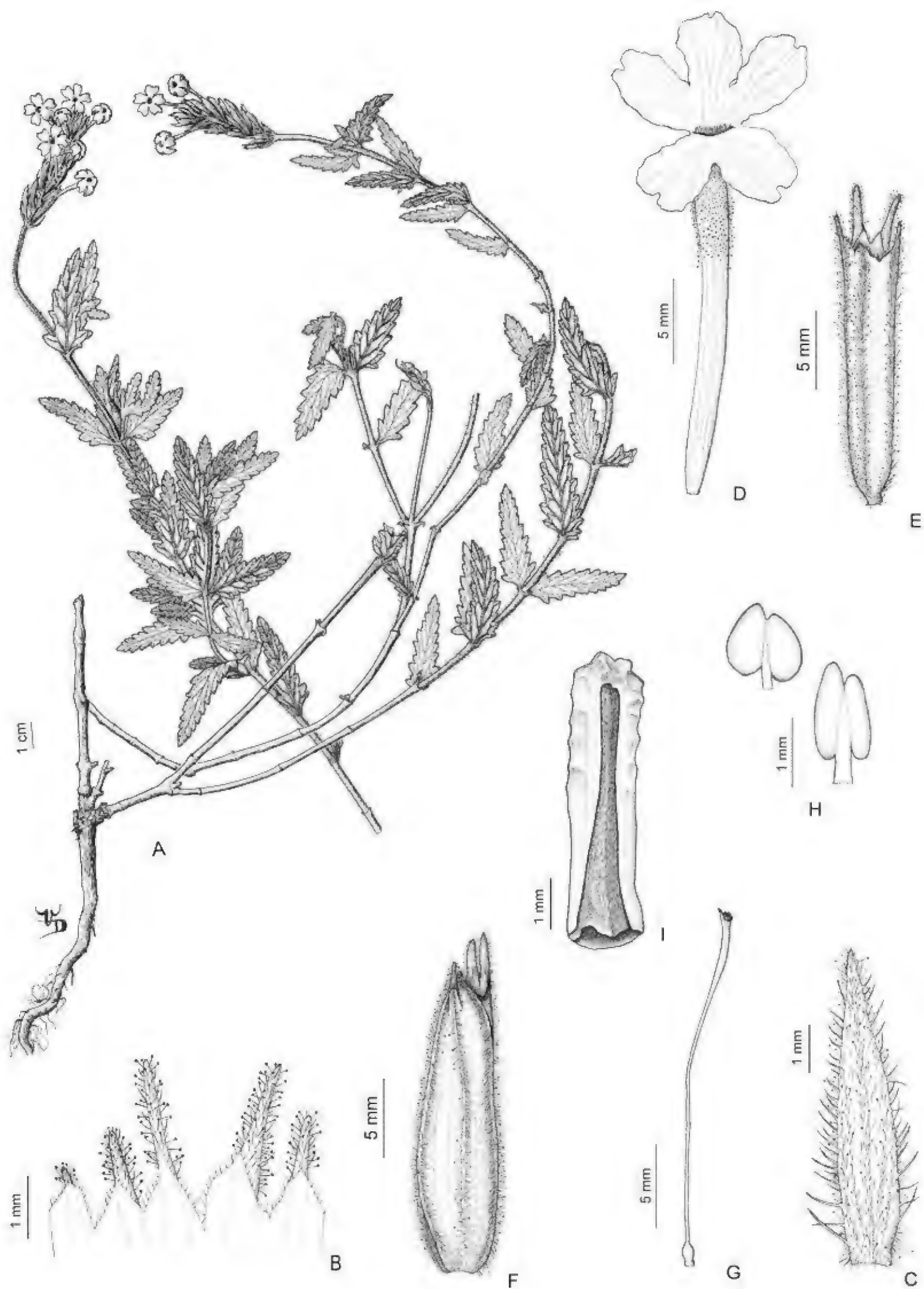


Figure 22. *Glandularia platensis* (Spreng.) Schnack & Covas. —A. Plant, general aspect. —B. Calyx extended, apical part, inner surface. —C. Floral bract. —D. Corolla. —E. Calyx. —F. Fructiferous calyx. —G. Gynoecia. —H. Superior pair of stamens. —I. Cluse, ventral face. A–I from *Burkart 23460* (SI).

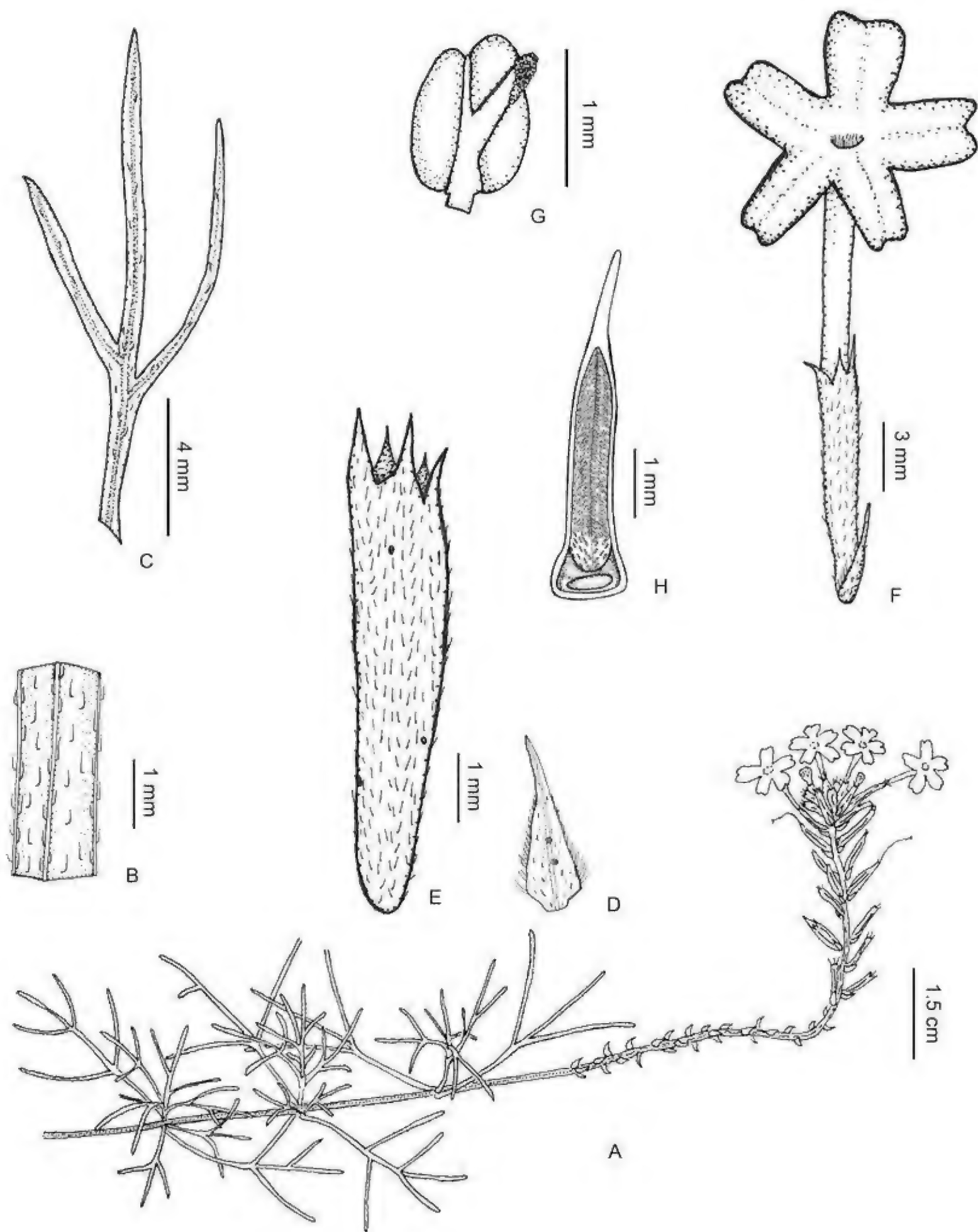


Figure 23. *Glandularia rectiloba* (Moldenke) P. Peralta & V. Thode. —A. Branch, general aspect. —B. Detail of stem pubescence. —C. Leaf, adaxial surface. —D. Floral bract. —E. Calyx. —F. Flower with floral bract. —G. Superior stamen. —H. Cluse, ventral face. A, B, H, from V. Thode 230 (ICN); C–G, from Krapovickas 22852 (TEX).

[2011: 390], P [bc] P000752585!; isoneotype, SI! fragm. ex P). Figure 22.

Verbena teucrioides Gillies & Hook., Bot. Misc. 1: 167. 1830. TYPE: Argentina. Mtns. of Mendoza, s.d., J. Gillies s.n. (lectotype, designated by Peralta & Múlgura [2011: 390], E [bc] E0000259074!).

Verbena scordioides Cham., Linnaea 7: 269. 1832. TYPE: Brazil. “Brazilia meridionalis,” s. loc., s.d., F. Sellow s.n. (lectotype, designated by Peralta & Múlgura [2011: 390], BR [bc] BR005503957!; isolectotypes, K [bc] K0000470552!).

Verbena chamaedryfolia Juss. f. *strigosa* Chodat, Bull. Herb. Boissier, sér. 2, 2: 818. 1902. *Verbena platensis*

Spreng. var. *stenodes* Briq., Bull. Herb. Boissier sér 2, 4: 1055. 1904. TYPE. Paraguay. Caragatatay, dic. [sine anno], *E. Hassler 5758* (lectotype, designated here, G [bc] G00077147!; isoelectotypes, G [bc] G00077145!, G [bc] G00077146!, G [bc] G00077178!, MPU [bc] MPU011496!, P [bc] P00650858!).

Verbena chamaedryfolia Juss. f. *foliosa* Chodat, Bull. Herb. Boissier, sér. 2, 2: 818. 1902. *Verbena platensis* Spreng. var. *latiuscula* Briq., nom. illeg. superfl., Bull. Herb. Boissier, sér. 2, 4: 1056. 1904. TYPE: Paraguay. Capibary, Sep., *E. Hassler 4428* (lectotype, designated by Peralta & Múlgura [2011: 391], K [bc] K00470722!).

Verbena platensis Spreng. f. *violacea* Moldenke, Phytologia 3(4): 177. 1949. TYPE: Uruguay. Soriano: Tala, Arroyo Grande, 3 Oct. 1895, *C. Osten 3195* (holotype, MVM!).

Plants suffruticose, 30–40 cm tall, stems decumbent with ascending floral branches, pubescence densely hirsute-glandular. Leaves sessile or briefly petiolate, petiole less than 10 mm, blade 20–60 × 10–20 mm, entire, narrowly ovate, apex acute, base cuneate, margin irregularly serrate, adaxial surface strigose, abaxial surface densely hispid-glandular. Inflorescences arranged in pleiobotrya, with frondose lateral paracladia, surpassing terminal inflorescence, inflorescences represented by dense multifloral spikes, enlarged in fruit, peduncles 10–70 mm. Floral bracts 4.5–7 mm, narrowly ovate, apex acute, hispid-glandular, ciliate margin. Calyx 10–17 mm, densely hirsute-glandular over the nerves, teeth aristate, 1–2 mm. Corolla 18–25 mm, externally villous with glandular hairs, white, sometimes pale pink at maturity. Superior pair of stamens unappendaged, style 21–22 mm. Cluses 4–4.5 mm, apex round.

Distribution and ecology. *Glandularia platensis* is widely distributed in northern and central Argentina and is also found in Bolivia, southern Brazil, and Uruguay. It grows in rocky fields, roadsides, sand, hills, clay soils, at elevations between 100 and 2200 m.

Notes. *Glandularia platensis* is distinguished by its hirsute-glandular pubescence, which makes it sticky, and its large white corolla (18–25 mm long) with externally glandular hairs.

There are four sheets belonging to the collection *Hassler 5758* housed in G. Following McNeill (2014) and McNeill et al. (2012), a suitable lectotype is designated among them. The chosen material has a label that reads exactly the same as in the protologue.

Selected material examined. BRAZIL. **Rio Grande do Sul:** Alegrete, Rio Ibirapuitá, *Arbo 2429* (CTES).

22. *Glandularia rectiloba* (Moldenke) P. Peralta & V. Thode, *Rodriguésia* 61(suppl.): 32. 2010. Basionym: *Verbena rectiloba* Moldenke, *Phytologia* 26: 409. 1973. TYPE: Brazil. Rio Grande do Sul: Rosário do Sul, on sandy banks of Rio Santa Maria, in Mun. Rosário do Sul, 20 Jan. 1973, *A. Krapovickas, C. Cristóbal & C. Quarín 22825* (holotype, TEX [bc] TEX0375268!; isotypes, CTES [bc] CTES0001675!, SI [bc] SI0003797!). Figure 23.

Prostrate herb, stems decumbent with ascending floral branches, pubescence glabrous to pilose. Leaves petiolate, petiole 11–15 mm, blade 30–55 × 20–40 mm, 3-sected, rarely bipinnatisect, segments linear, both surfaces scarcely strigose. Inflorescences arranged in monobotrya or pleiobotrya with frondose paracladia, surpassing principal inflorescence or not, inflorescences represented by dense multifloral spikes, enlarged in fruit, peduncle 15–20 mm. Floral bracts 2.5–4 mm, ovate, apex acute, pubescence strigose, ciliate margin. Calyx 9–11 mm, strigose with some patelliform glands, nerves not evident, teeth triangular, 0.5–1 mm. Corolla 14–18 mm, externally glabrous, violet. Superior pair of stamens with glandular appendages, surpassing thecae and corolla mouth, style 13–15 mm. Cluses 6–7 mm, apex rostrate.

Distribution and ecology. Only two collections of *Glandularia rectiloba* are known, both from the locality of Rosário do Sul, in Rio Grande do Sul, Brazil, found in the sandy banks of the Santa Maria River.

Notes. *Glandularia rectiloba* is similar to *G. tenera* in habit and in having sected leaves with linear segments. In *G. rectiloba*, the leaves are markedly 3-sected with bigger blades (30–55 × 20–40 mm vs. 15–20 × 15 mm) and longer petioles (11–15 mm vs. less than 10 mm). The corolla is bigger (14–18 mm vs. 8–9 mm), and the calyx does not have evident nerves as it does in most *Glandularia* species.

Selected material examined. BRAZIL. **Rio Grande do Sul:** Rosário do Sul, *V. Thode 230* (ICN).

23. *Glandularia scrobiculata* (Griseb.) Tronc., *Darwiniana* 19(3–4): 738. 1975. Basionym: *Verbena scrobiculata* Griseb., *Abh. Königl. Ges. Wiss. Göttingen* 24: 275. 1879. TYPE: Argentina. Jujuy: San Lorenzo, Oct. 1873, *P. G. Lorentz & G. Hieronymus 244* (holotype, GOET 00187!; isotype, CORD 6135!). Figure 24.

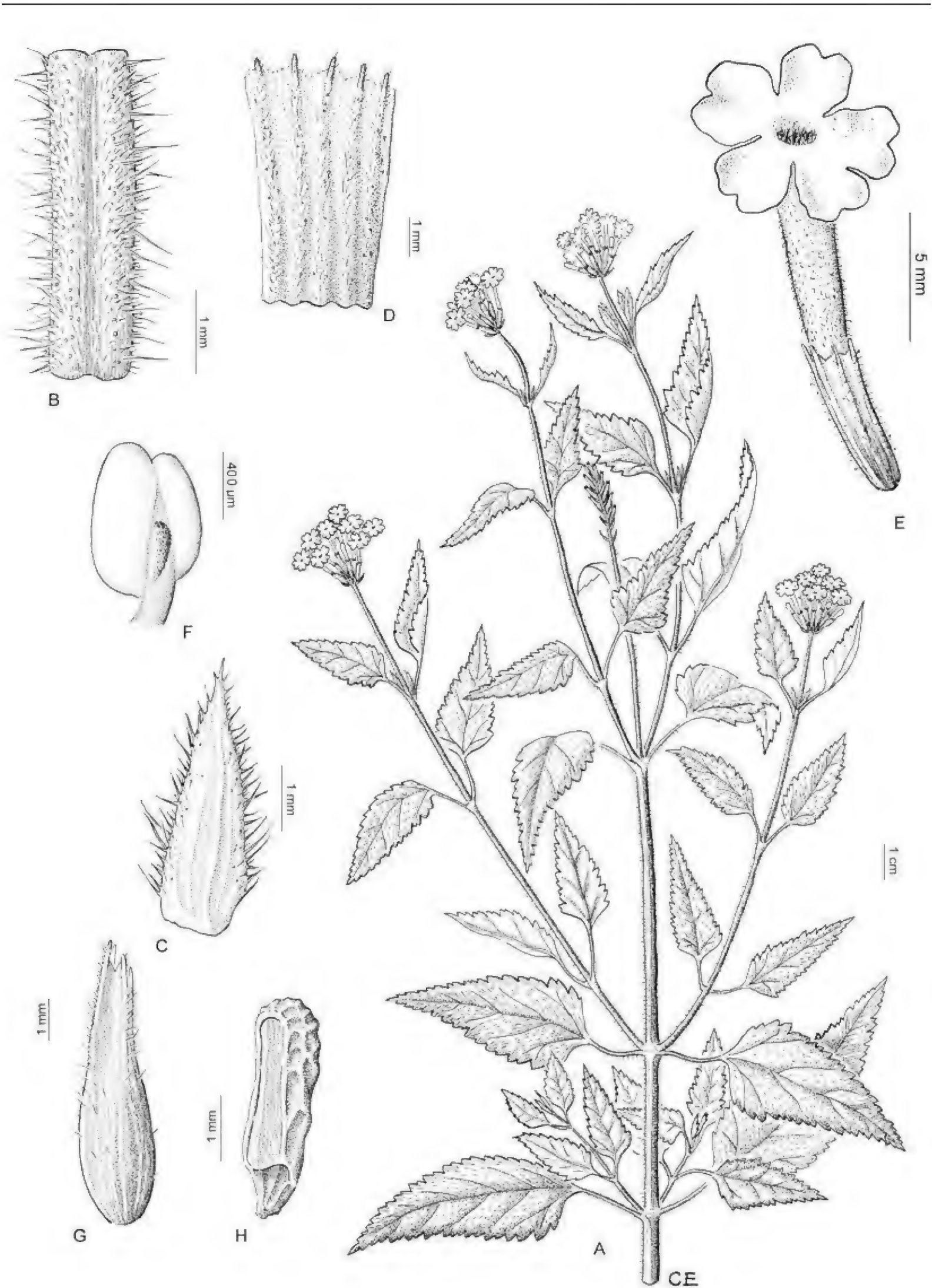


Figure 24. *Glandularia scrobiculata* (Griseb.) Tronc. —A. Branch, general aspect. —B. Detail of stem pubescence. —C. Floral bract. —D. Calyx extended, outer surface. —E. Flower. —F. Superior stamen. —G. Fructiferous calyx. —H. Cluse, ventral face. A–H from *Cabrera 28044* (SI).

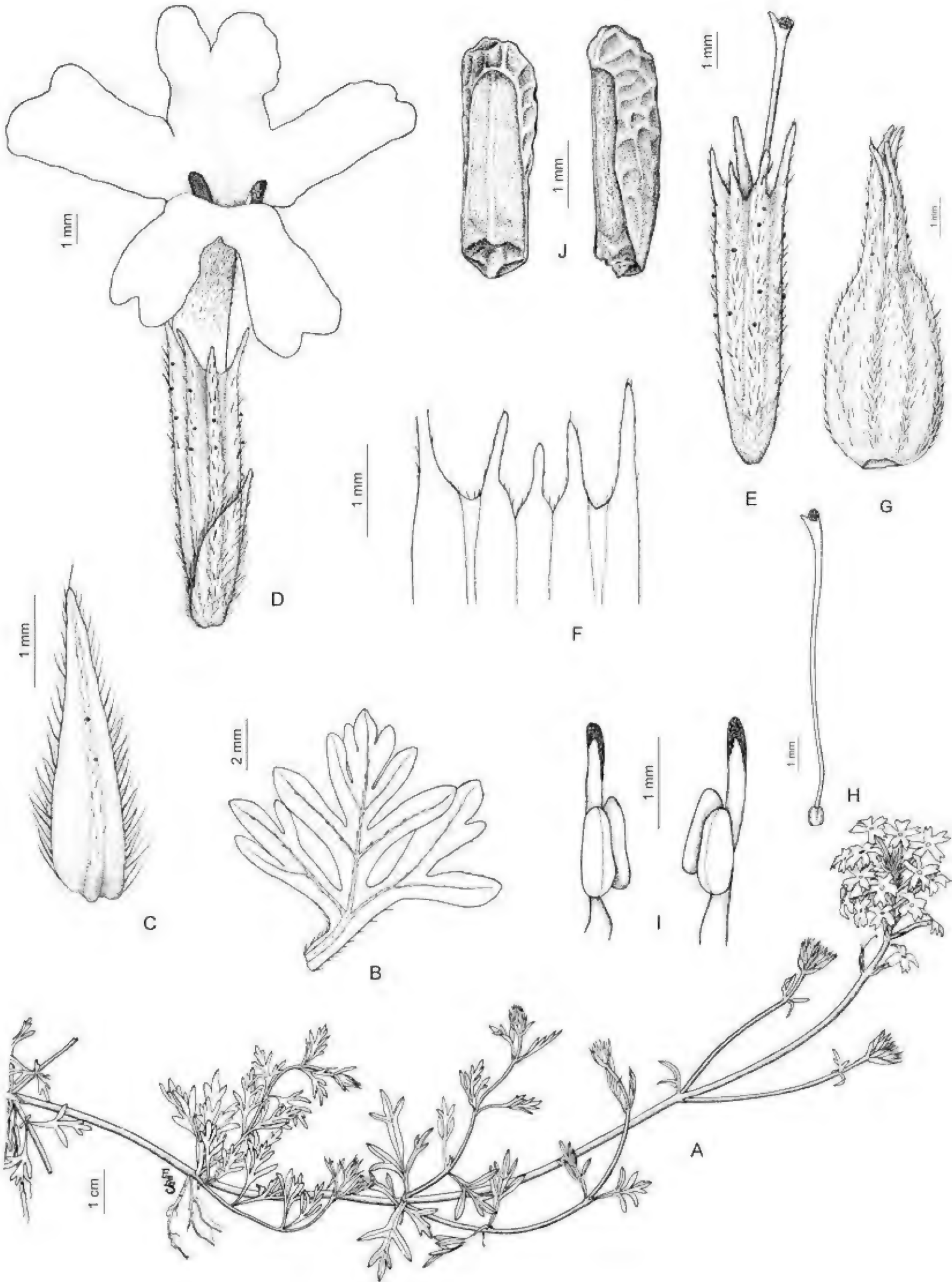


Figure 25. *Glandularia selloi* (Spreng.) Tronc. —A. Branch, general aspect. —B. Leaf, adaxial surface. —C. Floral bract. —D. Flower with floral bract. —E. Calyx. —F. Calyx extended, apical part, inner surface. —G. Fructiferous calyx. —H. Gynoecia. —I. Superior pair of stamens. —J. Cluses, ventral and lateral face. A–J from *Rosengurtt 2116* (SI).

Verbena hunzikeri Moldenke, Phytologia 2(8): 321. 1947. TYPE: Argentina. Tucumán: entre Alto del Clavillo y Alpachiri, 1800 m.s.m., 20 Sep. 1946, A. T. Hunziker 6812 (holotype, NY [bc] NY0138275!; isotypes, CORD [bc] CORD003847!, LIL [bc] LIL000184844!, SI [bc] SI00076259!).

Verbena moricolor Moldenke, Phytologia 2(10): 424. 1948. *Glandularia moricolor* (Moldenke) Tronc., nom. illeg. Darwiniana 18: 319. 1974. TYPE: Argentina: Jujuy, Ledesma, Sierra de Calilegua, 800 m.s.m., 11 Oct. 1927, S. Venturi 5397 (holotype, CAS [bc] CAS004922!; isotypes, BM [bc] BM000798318!, LIL [bc] LIL001438!, NY [bc] NY00138295!, S [bc] S04-2444!, SI [bc] SI003784!, US [bc] US00118716!).

Plants suffruticose, 50–100 cm tall, stems erect, 4-angled, pubescence hispid with glandular hairs. Leaves petiolate, petiole 15–25 mm, blade 40–65 × 15–40 mm, entire, sometimes trilobed toward base, ovate to triangular, apex acute, base truncate, margin irregularly serrate, adaxial surface strigose, abaxial surface hispid. Inflorescences arranged in pleiobotrya with frondose paracladia, surpassing principal inflorescence, inflorescences represented by dense multifloral spikes, enlarged in fruit, peduncles 30–45 mm. Floral bracts 3.5–6 mm, ovate, apex acute, subglabrous, with some glandular hairs, ciliate margin. Calyx 6.5–8 mm, hispid-glandular, teeth triangular, 0.5–1 mm. Corolla 11–12 mm, externally villous, violet or lilac. Superior pair of stamens with vestigial sessile glandular appendages, not surpassing thecae, not surpassing corolla mouth, style 10–11 mm. Cluses 2.8–3 mm, apex round.

Distribution and ecology. *Glandularia scrobiculata* is known from southern Bolivia, northern Argentina, and southern Brazil. It grows in forest margins and roadsides, at elevations between 250 and 2000 m.

Notes. *Glandularia scrobiculata* is similar to *G. hasslerana* and *G. nana*. See differences in notes under each species. In dried herbarium material, *G. scrobiculata* usually presents with the adaxial surface darker than the abaxial surface.

Selected material examined. BRAZIL. Rio Grande do Sul: Nova Roma do Sul, Nov. 2004, Larocca s.n. (PACA 97350).

24. *Glandularia selloi* (Spreng.) Tronc., Darwiniana 13(2–4): 481. 1964. Basionym: *Verbena selloi* Spreng., Syst. Veg. (ed. 16) [Sprengel] 2: 750. 1825. *Shuttleworthia selloi* (Spreng.) Walp., Repert. Bot. Syst. [Walpers] 4: 13. 1845. TYPE: Brazil. s. loc., s.d., F. Sellow s.n. [ex Herb. Imperial du Brésil 549] (lectotype, designated

by Peralta & Múlgura [2011: 393], P [bc] P00650862!). Figure 25.

Prostrate herbs, stems decumbent with ascending floral branches, pubescence glabrous to hispid, retrorse hairs. Leaves briefly petiolate, petiole 3.5–5 mm, blade 7–20 × 5–15 mm, 3-sected to bipinnatifid, ovate, segments ovate, obovate, apex acute, base attenuate, margin irregularly lobate, adaxial surface lightly strigose, abaxial surface hispid over nerves. Inflorescences arranged in monobotrya or frondose pleiobotrya, lateral paracladia surpassing principal inflorescence, inflorescences represented by dense multifloral spikes, enlarged in fruit, peduncles 5–15 mm. Floral bracts 4–5 mm, narrowly ovate, apex acute, glabrous with hispid hairs over central nerve, ciliate margin. Calyx 7–8 mm, hispid, with some patelliform glands, teeth acute, 1–2 mm. Corolla 15 mm, externally villous, lilac or pink. Superior pair of stamens with glandular appendages, surpassing thecae, surpassing corolla mouth, style 8–10 mm. Cluses 3–3.5 mm, apex round.

Distribution and ecology. *Glandularia selloi* is widely distributed in Uruguay and southern Brazil. In Argentina it is present only in the province of Entre Ríos. It grows on beaches, sand dunes, roadsides, swamps, and disturbed areas.

Notes. *Glandularia selloi* is similar to *G. subincana*. The latter is distinguished by its externally glabrous corollas; the corollas in *G. selloi* are villous. It is also similar to *G. catharinae* and *G. tenera*; see notes under these taxa.

Selected material examined. BRAZIL. Rio Grande do Sul: Coxilho Pedras Altas, Pedersen 11445 (CTES, SI).

25. *Glandularia sessilis* (Cham.) Tronc., Fl. Il. Entre Rios, Colecc. Ci. Inst. Nac. Tecnol. Agropecu. 6(5): 247. 1979. Basionym: *Verbena stellarioides* Cham. var. *sessilis* Cham., Linnaea 7: 265. 1832. *Verbena sessilis* (Cham.) Kuntze, Revis. Gen. Pl. 3(3): 257. 1898. TYPE: Brazil. s. loc., s.d., F. Sellow 1563 (lectotype, designated by Peralta & Múlgura [2011: 394], G). Figure 26.

Verbena kuhlmannii Moldenke, Phytologia 31(1): 29. 1975. TYPE: Brazil. São Paulo: Lake Moji-Guaçu, Reserva Florestal (faz. Campininha), 27 Oct. 1955, M. Kuhlmann 3717 (holotype, US [bc] US00118708!; isotype, SI [bc] SI0030060!).

Verbena tristachya Tronc. & Burkart, Darwiniana 7: 208. 1946. *Glandularia tristachya* (Tronc. & Burkart) Schnack & Covas, syn. nov. Bol. Soc. Argent. Bot. 1: 284. 1946. TYPE: Argentina. Entre Ríos: Dpto. Ibicuy, Delta superior, Isla de las Lechiguanas, 30

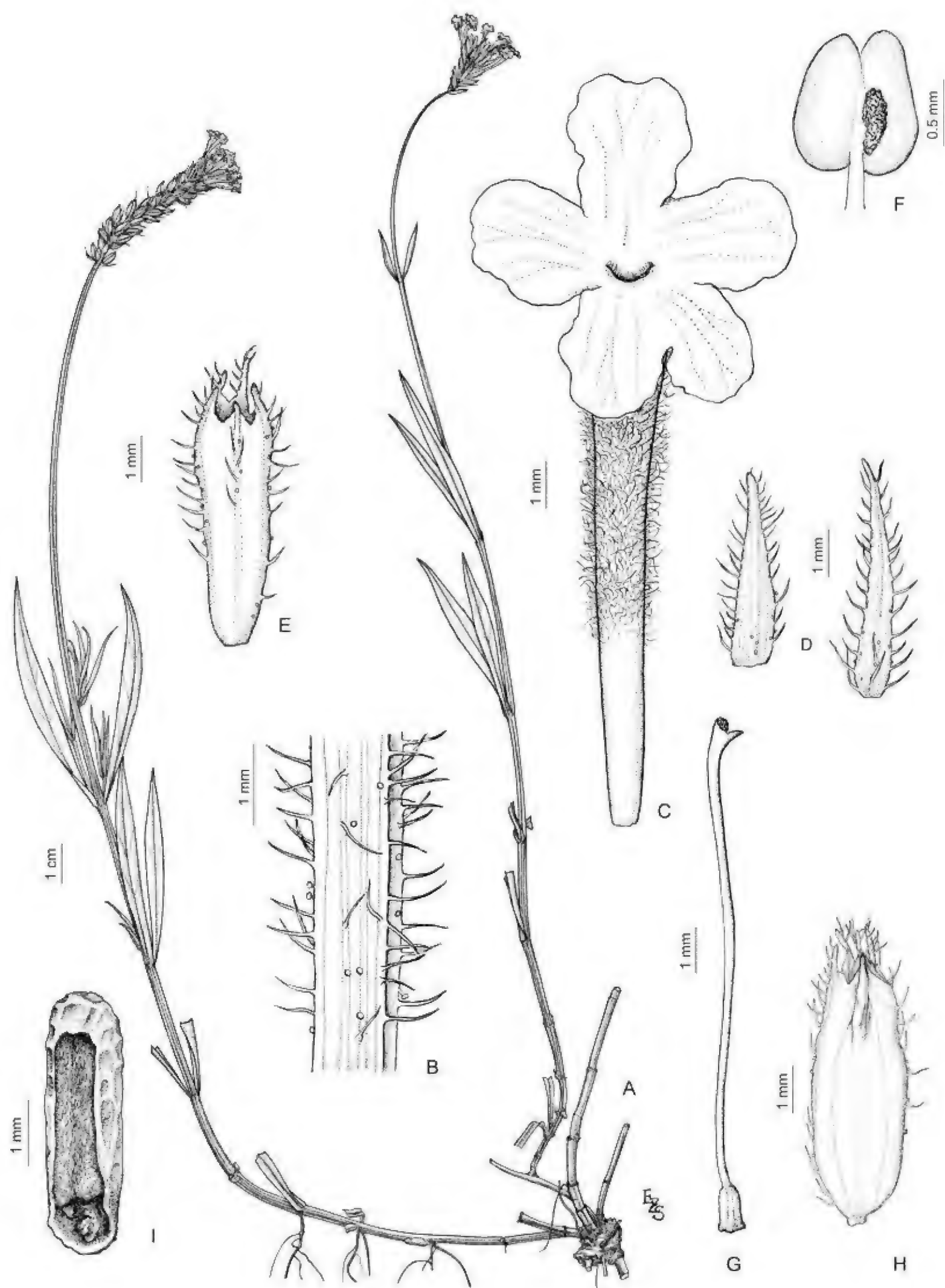


Figure 26. *Glandularia sessilis* (Cham.) Tronc. —A. Plant, general aspect. —B. Detail of stem pubescence. —C. Corolla. —D. Floral bracts. —E. Calyx. —F. Superior stamen. —G. Gynoecia. —H. Fructiferous calyx. —I. Cluse, ventral face. A–I from Pedersen 7171 (SI).

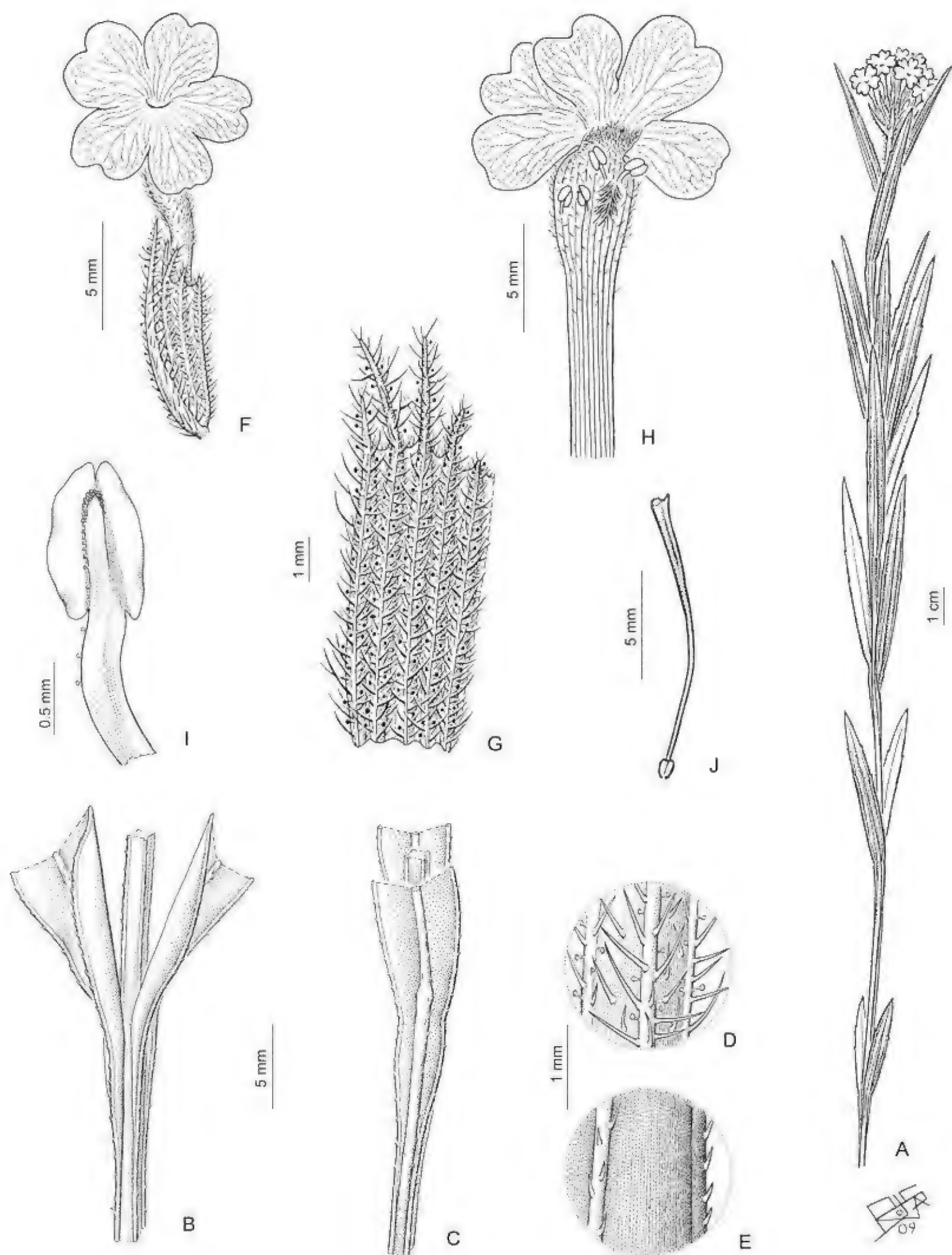


Figure 27. *Glandularia stellarioides* (Cham.) Schnack & Covas. —A. Plant, general aspect. —B, C. Detail of leaf base. —D. Detail of leaf pubescence, abaxial surface. —E. Detail of leaf pubescence, abaxial surface. —F. Flower with floral bract. —G. Calyx extended, outer surface. —H. Corolla opened with androecia. —I. Superior stamen. —J. Gynoecia. A–J from *Montes 15449* (SI).

Dec. 1945, *A. Burkart 15644* (holotype, SI [bc] SI003798!; isotypes, K [bc] K00470705!, K [bc] K00470704!, NY [bc] NY00138343!, SI [bc] SI003800!, US [bc] US00118741!).

Verbena morongii Britton, Ann. New York Acad. Sci. 7: 192. 1892. TYPE: Paraguay. Central: Caballero, 21 Jan. 1889, *T. Morong 600* (holotype, NY [bc] NY00138296!; isotypes, PH [bc] PH0028760!, US [bc] US00118717!).

Plants suffruticose plants, 40–80 cm tall, stems erect or decumbent with ascending floral branches, pubescence glabrous or slightly strigose, with patelliform glands. Leaves sessile, blade 40–100 × 5–10 mm, entire, linear to narrowly elliptic, apex acute, base cuneate, margin entire or slightly serrate, both surfaces glabrous or slightly strigose. Inflorescences arranged in monobotrya or pleiobotrya with frondose paracladia, surpassing principal inflorescence, inflorescences represented by dense multifloral spikes, enlarged in fruit, peduncles 20–40 mm. Floral bracts 5–7 mm, narrowly ovate, apex acute, subglabrous, long ciliate margin. Calyx 5–8 mm, glabrous, hispid over nerves, teeth acute, 1–1.5 mm. Corolla 12–13 mm, externally villous, violet or blue. Superior pair of stamens with sessile glandular appendages, not surpassing thecae, not surpassing corolla mouth, style 11 mm. Cluses 3 mm, apex round.

Distribution and ecology. *Glandularia sessilis* is found in northeastern Argentina, Paraguay, southern Brazil (*Verbena kuhlmannii* type material from São Paulo), and Uruguay. It grows in grasslands, flooded areas, and swamps.

Notes. *Glandularia sessilis* is similar to *G. stellarioides*. The latter is distinguished by its decurrent leaf base and the presence of longer floral bracts (10–14 mm long vs. 5–7 mm long).

Peralta (2009) differentiates *Glandularia sessilis* from *G. tristachya* by the presence of sessile glandular appendages in the stamens and longer floral bracts in the former. However, the analysis of type material and additional specimens has led to the conclusion that these are the same species.

Selected material examined. BRAZIL. **Rio Grande do Sul:** Bagé, *Thode 111* (ICN).

26. *Glandularia stellarioides* (Cham.) Schnack & Covas, Bol. Soc. Argent. Bot. 1: 284. 1946. Basionym: *Verbena stellarioides* Cham., Linnaea 7: 264. 1832. TYPE: Brazil. s. loc., s.d., *F. Sellow s.n.* (lectotype, designated by Peralta & Múlgura [2011: 395], HAL [bc] HAL00098274!). Figure 27.

Plants suffruticose, 40–70 cm tall, stems erect or decumbent with ascending floral branches, pubescence glabrous or slightly strigose over the ribs. Leaves sessile, blade 25–100 × 5–6 mm, entire, linear to narrowly elliptic, apex acute, base decurrent, margin entire or slightly serrate, both surfaces glabrous or slightly strigose. Inflorescences arranged in monobotrya or pleiobotrya with frondose paracladia, surpassing principal inflorescence, inflorescences represented by dense multifloral spikes, enlarged in fruit, peduncles 10–30 mm. Floral bracts 10–14 mm, narrowly ovate, apex acute, strigose, ciliate margin. Calyx 8.5–10 mm, densely hispid with glandular hairs, teeth acute or aristate, 2 mm. Corolla 15 mm, externally villous, lilac or pink. Superior pair of stamens with vestigial sessile glandular appendages, not surpassing thecae, not surpassing corolla mouth, style 12 mm. Cluses 3–3.5 mm, apex round.

Distribution and ecology. *Glandularia stellarioides* is distributed in northeastern Argentina and Rio Grande do Sul, Brazil. It inhabits grasslands and flooded fields at sea level.

Notes. *Glandularia stellarioides* is similar to *G. sessilis*; see differences under the latter species.

Selected material examined. BRAZIL. **Rio Grande do Sul:** Tupanciretan, Chacara, *Rambo 9950* (LIL).

27. *Glandularia subincana* Tronc., Darwiniana 13(2–4): 478. 1964. TYPE: Uruguay. Salto: Río Arapey, Arroyo Valentín, 28 Jan. 1937, *B. Rosengurtt B-992* (holotype, SI [bc] SI003810!, isotypes, MVFA [bc] MVFA0000756!, NY [bc] NY00137546!). Figure 28.

Plants suffruticose, 8–40 cm tall, stems decumbent with ascending floral branches, pubescence hispid, more dense toward apex, retrorse hairs. Leaves sessile, or briefly petiolate, petiole less than 5 mm, blade 10–30 × 10–25 mm, 3-dissected, segments narrowly ovate, lobate, apex acute-obtuse, base attenuate, adaxial surface hirsute with glandular hairs, abaxial surface densely hirsute over nerves. Inflorescences arranged in monobotrya or pleiobotrya with frondose paracladia, surpassing principal inflorescence, inflorescences represented by dense multifloral spikes, enlarged in fructification, peduncles 20–50 mm. Floral bracts 4–5 mm, narrowly ovate, apex acute, hirsute with patelliform glands, ciliate margin. Calyx 8–8.5 mm, slightly strigose with patelliform glands, teeth triangular, 1 mm. Corolla 12–15 mm, externally glabrous, violet, lilac, or blue. Superior pair of stamens with sessile glandular

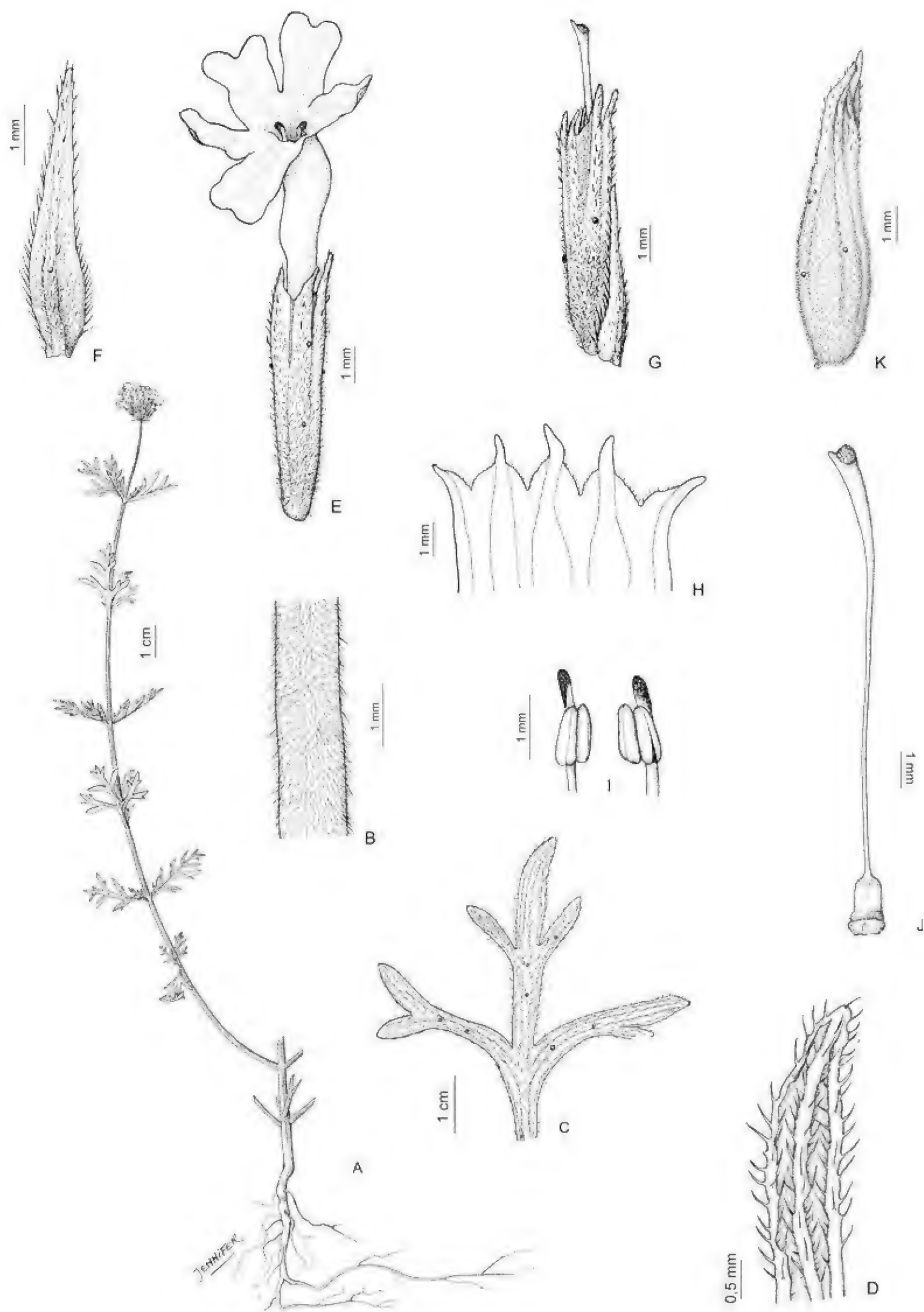


Figure 28. *Glandularia subincana* Tronc. —A. Plant, general aspect. —B. Detail of stem pubescence. —C. Leaf, abaxial surface. —D. Detail of leaf abaxial pubescence, surface. —E. Flower. —F. Floral bract. —G. Calyx with floral bract. —H. Calyx extended, apical part, inner surface. —I. Superior pair of stamens. —J. Gynoecia. —K. Fructiferous calyx. A–K from Morrone 5806 (SI).

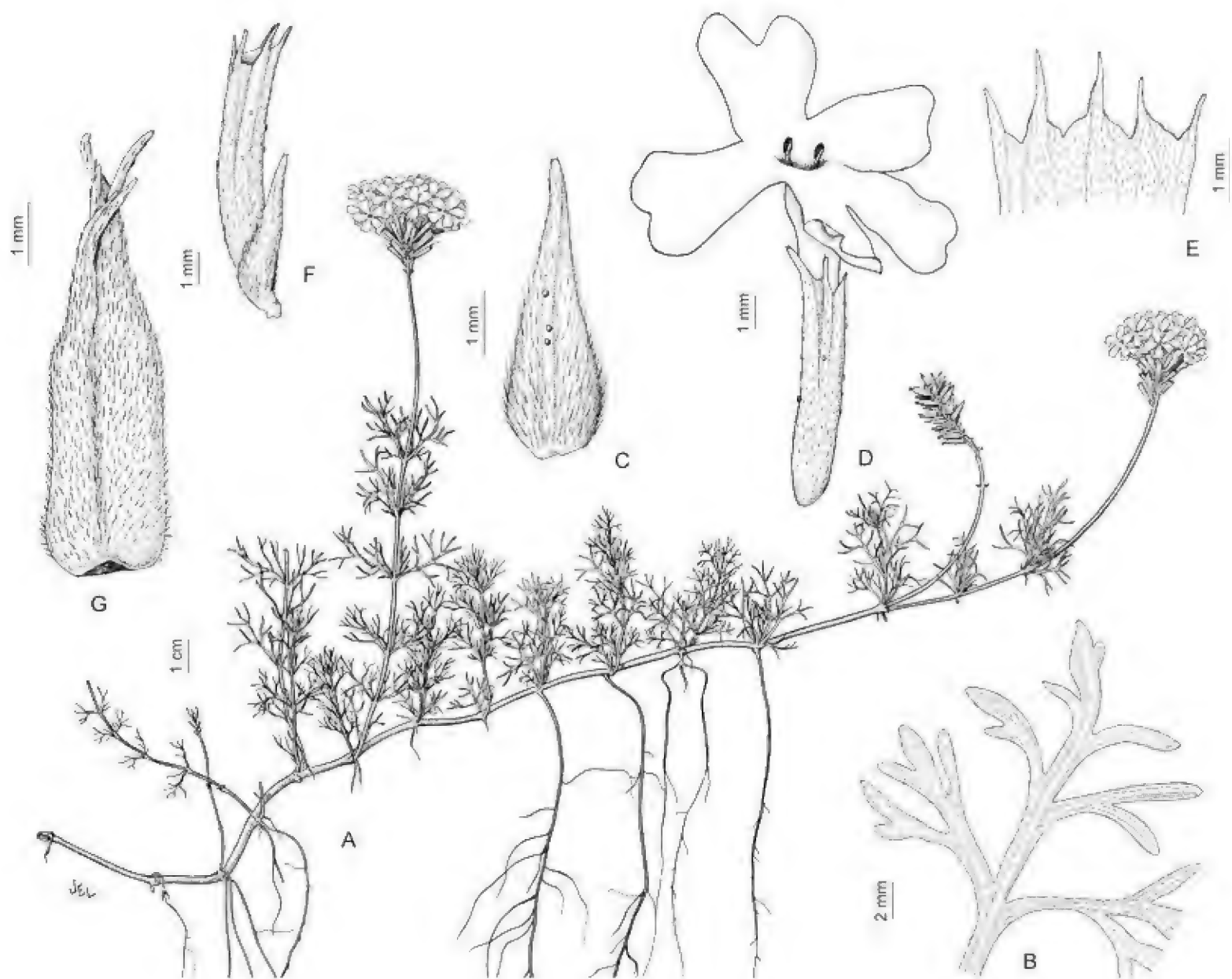


Figure 29. *Glandularia tenera* (Spreng.) Cabrera. —A. Plant, general aspect. —B. Leaf, abaxial surface. —C. Floral bract. —D. Flower. —E. Calyx extended, apical part, outer surface. —F. Calyx with floral bract. —G. Fructiferous calyx. A–G from Ragonese 49 (SI).

appendages, surpassing thecae and corolla mouth, style 8–9 mm. Cluses 2.5–3 mm, apex round.

Distribution and ecology. It grows in northern and central Argentina, southern Brazil, and Uruguay. It can be found in slopes and sandy soils, at elevations from sea level to 350 m.

Notes. *Glandularia subincana* is similar to *G. tomophylla*; it is distinguished by the corolla pubescence, which is glabrous in the former and externally villous in the latter. It is also similar to *G. selloi* and *G. tenera*; see differences under these species.

Selected material examined. BRAZIL. **Rio Grande do Sul:** Santana do Livramento, *Schneider 1612* (ICN).

28. *Glandularia tenera* (Spreng.) Cabrera, Man. Fl. Alrededores Buenos Aires: 398. 1953. Basionym: *Verbena tenera* Spreng., Syst. Veg. (ed. 16) [Sprengel] 2: 750. 1825. TYPE: Uruguay. Montevideo, s.d., *F. Sellow* s.n. (lectotype,

designated by Peralta & Múlgura [2011: 397], K [bc] K00470522!; isoelectotypes, E [bc] E000373267!, K [bc] K00470523!). Figure 29.

Verbena pulchella Sweet, Brit. Fl. Gard. [Sweet], ser. 1, 3: tab. 295. 1827. *Shuttleworthia pulchella* (Sweet) Meisn., Pl. Vasc. Gen. [Meisner], 2: 198. 1840. *Glandularia pulchella* (Sweet) Tronc., Darwiniana 13(2–4): 473. 1964. TYPE: tab. 295, in Sweet, 1827. Brit. Fl. Gard. ser. 1, 3.

Verbena tenera Spreng. var. *albiflora* Kuntze, Revis. Gen. Pl. 3(2): 258. 1898. *Verbena tenera* f. *albiflora* (Kuntze) Moldenke, Phytologia 41: 451. 1979. TYPE: Argentina. Santa Fe: Ceres, Oct. 1892, *C. E. O. Kuntze* s.n. (holotype, NY [bc] NY000138335!; isotypes, F [bc] F0074535!, LP!).

Glandularia pulchella (Sweet) Tronc. var. *clavellata* Tronc., Darwiniana 13(2–4): 476. fig. 3. 1964. *Verbena pulchella* Sweet var. *clavellata* (Tronc.) Shinnars, Sida 2(3): 266. 1966. TYPE: Argentina. Buenos Aires: Sierra de la Ventana, Parque Provincial, 6 Oct. 1939, *A. L. Cabrera 5288* (holotype, SI!).

Glandularia pulchella (Sweet) Tronc. var. *gracilior* Tronc., Darwiniana 13(2–4): 476. 1964. *Verbena pulchella* Sweet var. *gracilior* (Tronc.) Shinnars, Sida 2(3): 266. 1966. TYPE: Argentina. Buenos Aires: Pdo. General Madariaga [Pdo. Villa Gesell], Villa Gesell, 5 Mar.

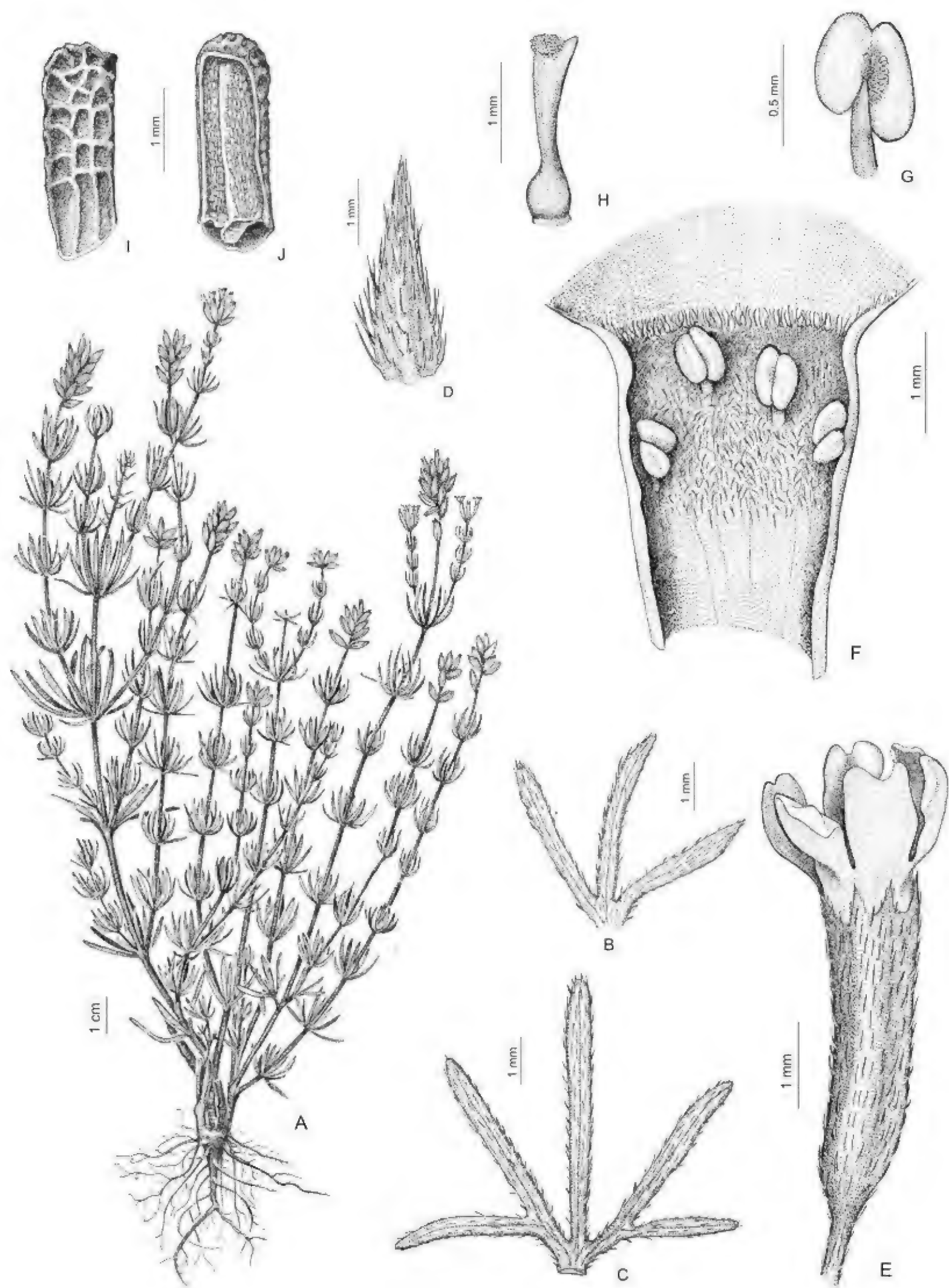


Figure 30. *Glandularia thymoides* (Cham.) N. O’Leary. —A. Plant, general aspect. —B, C. Leaves, adaxial surface. —D. Floral bract. —E. Flower. —F. Corolla opened with androecia. —G. Superior stamen. —H. Gynoecia. —I. Cluse, dorsal face. —J. Cluse, ventral face. A–J from Troncoso and Bacigalupo (1982).

1961, *A. Burkart* 22380 (holotype, SI-76238!; isotype, US [bc] US00118729!).

Verbena santiaguensis (Covas & Schnack) Moldenke f. *albiflora* Moldenke, *Phytologia* 18: 295. 1969. TYPE: Argentina. Buenos Aires: Pdo. General Pueyrredón, [Mar del Plata] Playa Grande, 10 Dec. 1944, *J. M. Villegas Vaquero* 666 (holotype, NY [bc] NY000138321!).

Prostrate herb, stems decumbent with ascending floral branches, pubescence strigose. Leaves briefly petiolate, petiole less than 10 mm, blade 15–20 × 15 mm, 3- to 5-dissected to bipinnatisect, segments linear to narrowly ovate, both surfaces strigose with patelliform glands on abaxial surface. Inflorescences arranged in monobotrya or pleiobotrya with frondose paracladia, surpassing principal inflorescence, inflorescences represented by dense multifloral spikes, enlarged in fruit, peduncle 15–20 mm. Floral bracts 3.5–4.5 mm, ovate, apex acute, pubescence strigose, with patelliform glands. Calyx 8–9 mm, strigose with some patelliform glands, teeth acute, 1 mm. Corolla 12–13 mm, externally glabrous, violet. Superior pair of stamens with glandular appendages, surpassing thecae and corolla mouth, style 11 mm. Cluses 4–6 mm, apex rostrate.

Distribution and ecology. *Glandularia tenera* is found in northern and central Argentina, Paraguay, Uruguay, and southern Brazil, in the states of Rio Grande do Sul, Santa Catarina, and São Paulo. It grows in sandy fields, roadsides, margins of streams and rivers, and rocky areas, at elevations between sea level and 560 m.

Notes. *Glandularia tenera* is similar to *G. selloi* and *G. subincana*. It is distinguished by its rostrate apex cluse, which is round in the latter two species. It can also be confused with *G. aristigera* and *G. rectiloba*; see differences under these species.

Selected material examined. BRAZIL. **Rio Grande do Sul:** Ibirubá, *Thode* 67 (ICN). **Santa Catarina:** Araranguá, *Reitz c1280e* (SI). **São Paulo:** Piracicaba, Sep. 2005, *Andrade s.n.* (ESA 50747).

29. *Glandularia thymoides* (Cham.) N. O'Leary, *Novon* 17(4): 509. 2007. Basionym: *Verbena thymoides* Cham., *Linnaea* 7: 257. 1832. TYPE: Brazil. s. loc., s.d., *F. Sellow s.n.* (lectotype, designated by O'Leary et al. [2007a: 509], K [bc] K000470527!; isoelectotypes, BR [bc] BR0000005503964!, G [bc] G00366712!, F-876157!, HAL-98272!, K [bc] K000470526!, M [bc] M0111658!, NY [bc] NY00138338!). Figure 30.

Verbena thymoides Cham. f. *albiflora* Moldenke, *Phytologia* 3(4): 178. 1949. TYPE: Uruguay. Dpto. Minas: Cerro Nico Pérez y Sierra Tapambay, Nov.–Dec. 1892, *Arechavaleta 11/1982* (holotype, MVM; isotype, NY-3233, fragm. ex MVM!).

Plants suffruticose, prostrate, 20–30 cm tall, stems decumbent with ascending floral branches, pubescence strigose. Leaves sessile, blade 5–10 × 0.2–1 mm, trisected, segments linear or narrowly elliptic, lateral segments usually biparted or bisected, apex acuminate, margins entire, usually revolute, pubescence strigose on both surfaces. Inflorescences arranged in monobotrya or frondose pleiobotrya, lateral paracladia surpassing terminal inflorescence, inflorescences represented by dense multifloral spikes, enlarged in fruit, peduncle 10 mm. Floral bracts 1.8–3 mm, narrowly ovate, apex acute, sparsely strigose, glabrous margins. Calyx 3–4 mm, sparsely strigose, teeth triangular, 1 mm. Corolla 4–5.5 mm, externally glabrous, pale blue or lilac turning white to violet. Superior pair of stamens with vestigial glandular appendages or unappendaged, not surpassing thecae, not surpassing corolla mouth; style 1.5–2 mm. Cluses 2 mm, apex round.

Distribution and ecology. *Glandularia thymoides* occurs in Argentina in the province of Entre Ríos as well as in southern Brazil in the states of Rio Grande do Sul, Santa Catarina, Paraná, and São Paulo. It is also found in Uruguay. It is found in dry fields and rocky and sandy soils, generally with grasses.

Notes. *Glandularia thymoides* is morphologically similar to *G. balansae*; these species share the presence of trisected leaves with linear or narrowly elliptic segments and small flowers with short calyx and corolla. Troncoso and Bacigalupo (1982) differentiated these species by the length of the leaves, the presence or absence of glandular appendages in the anthers, and the comparative length of the floral bracts, calyx, and style. *Glandularia balansae* has a different habit; it is more erect, while *G. thymoides* is prostrate. Finally, *G. balansae* grows in Paraguay and northeastern Argentina, in the provinces of Misiones and Corrientes, while *G. thymoides* is found in southern and eastern Argentina, reaching Entre Ríos Province and Uruguay. They coexist in southern Brazil (Moldenke, 1962; Troncoso & Bacigalupo, 1982).

Selected material examined. BRAZIL. **Paraná:** Palmeira, Córrego da Anta, 2 Feb. 1975, *Pedersen s.n.* (CTES 354603). **Rio Grande do Sul:** Torres, Butiazal, *Hagelund 15027* (CTES). **Santa Catarina:** Sombrio, *Rambo 32003* (SI). **São Paulo:** Itararé, *Miyagi et al.* 600 (ESA).

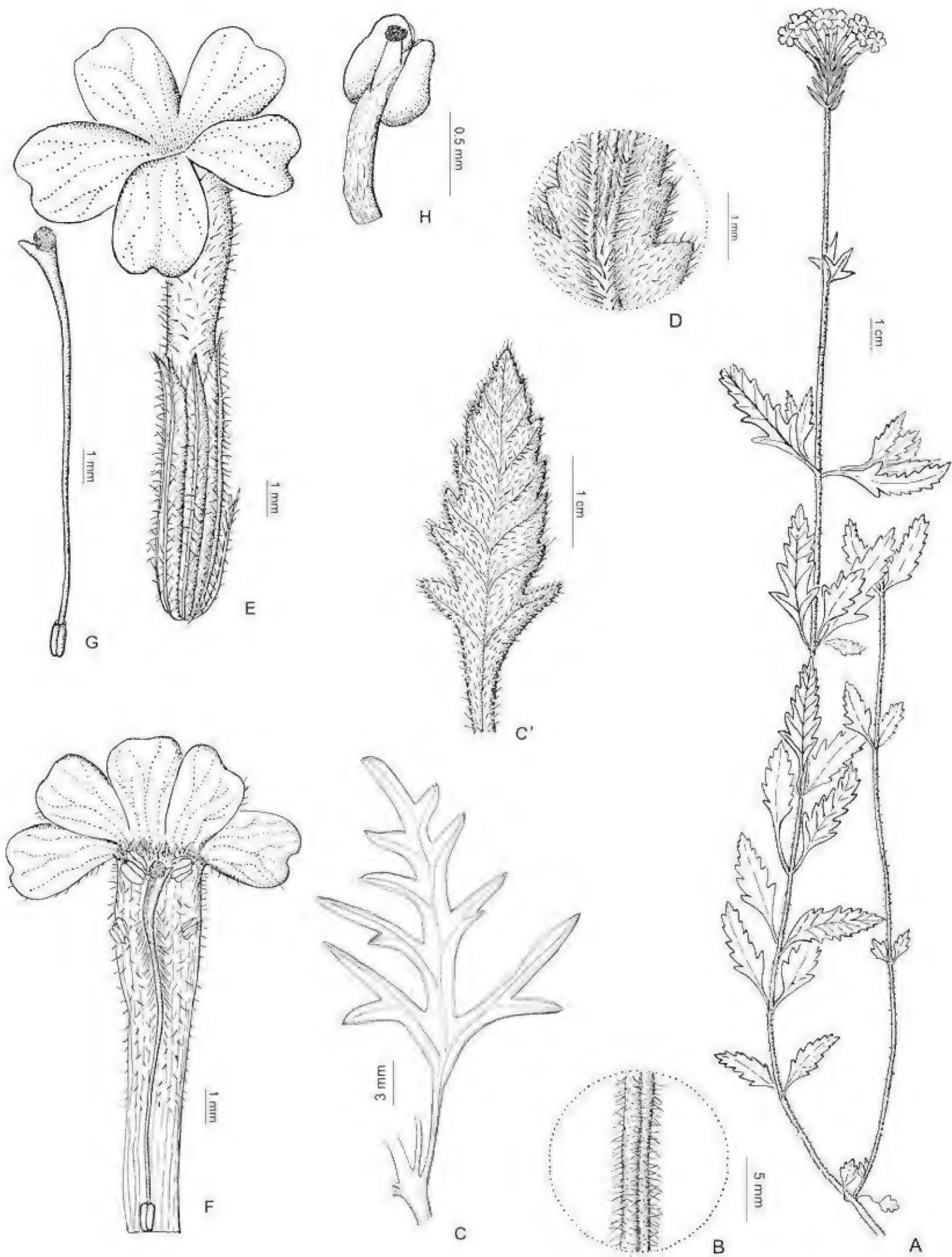


Figure 31. *Glandularia tomophylla* (Briq.) N. O’Leary & V. Thode —A. Branch, general aspect. —B. Detail of stem pubescence. —C, C’. Leaves, adaxial surface. —D. Detail of leaf pubescence, abaxial surface. —E. Flower with floral bract. —F. Corolla opened with androecia and gynoecia. —G. Gynoecia. —H. Superior stamen. A–H from *Ahumada* 4105 (SI).

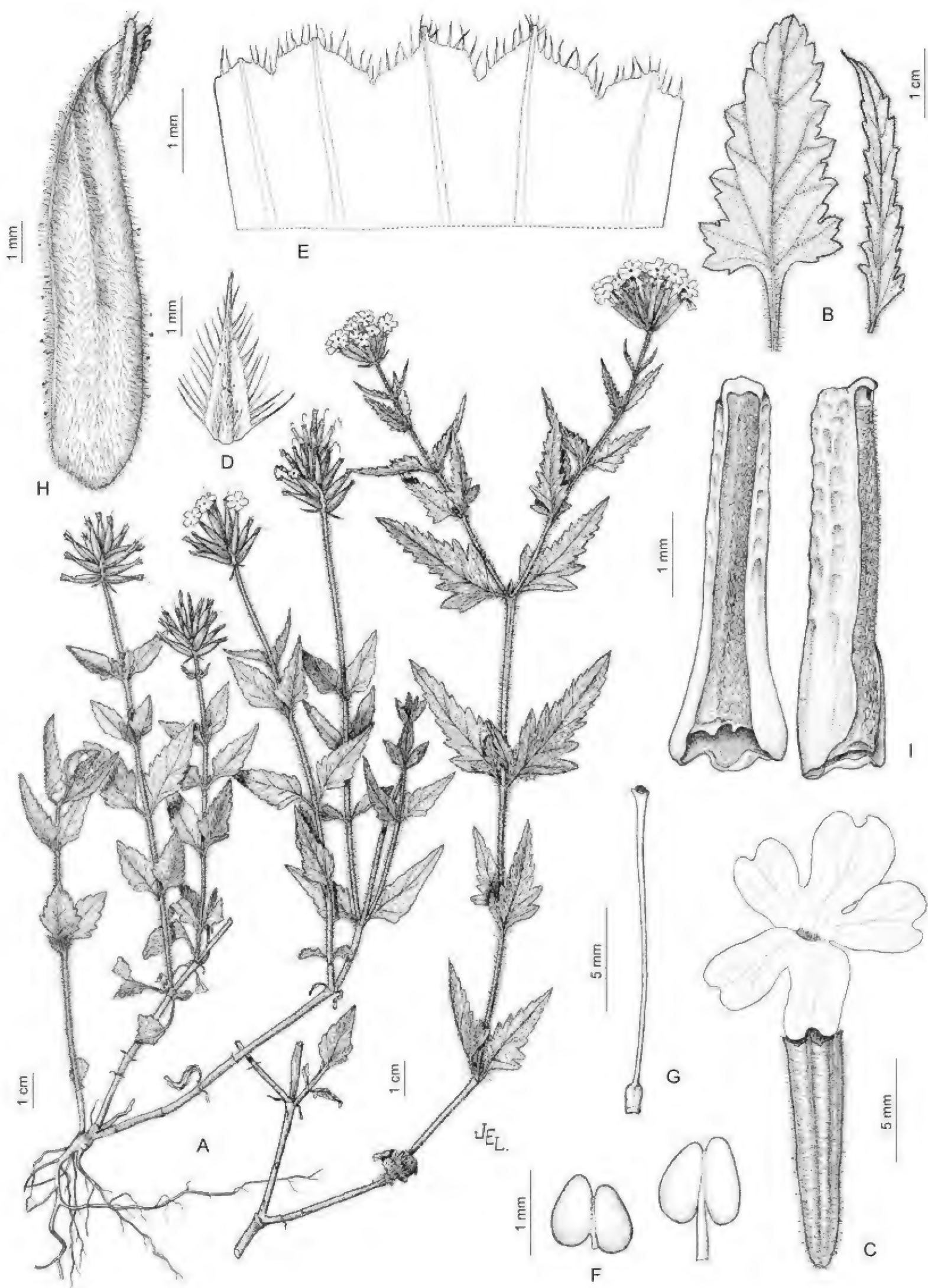


Figure 32. *Glandularia tweediana* (Niven ex Hook.) P. Peralta. —A. Plant, general aspect. —B. Leaves, adaxial surface. —C. Flower. —D. Floral bract. —E. Calyx extended, apical part, inner surface. —F. Superior pair of stamens. —G. Gynoecia. —H. Fructiferous calyx. —I. Cluses, ventral and lateral face. A–I redrawn from Troncoso (1979).

30. *Glandularia tomophylla* (Briq.) N. O'Leary & V. Thode, nov. comb. *Darwiniana* 45(2): 241. 2007. Basionym: *Verbena tomophylla* Briq., Bull. Herb. Boissier sér. 2, 4: 1061. 1904. TYPE: Paraguay. Caragatatay, Oct. 1898/1899, *E. Hassler* 3295 (holotype, G; isotypes, GH!, K [bc] K000470721!, P [bc] P00752581!, SI-76331, fragm. ex G!). Figure 31.

Verbena megapotamica Spreng. var. *pinnatiloba* Kuntze, Revis. Gen. Pl. 3(2): 256. 1898. *Verbena pinnatiloba* (Kuntze) Moldenke, Phytologia 2: 28. 1941. TYPE: Paraguay. s. loc., Sep. 1892, *E. O. Kuntze* s.n. (holotype, NY not seen; isotypes, SI-76307! fragm. ex NY!, US-701063!).

Verbena calliantha Briq., Bull. Herb. Boiss., sér. 2, 4: 1059. 1904. TYPE: Paraguay. Concepción: in Dumetis, Oct., *E. Hassler* 7615 (lectotype, designated by Peralta & Múlgura [2011: 399], NY [bc] NY00138249!; isolectotype, BM [bc] BM000098802!).

Verbena calliantha Briq. var. *microsoma* Briq., Bull. Herb. Boiss., sér. 2, 4: 1060. 1904. TYPE: Paraguay. Cerro Pyta, Oct. sine anno, *E. Hassler* 1272 (holotype, G not seen).

Verbena storeoclada Briq., Bull. Herb. Boiss., sér. 2, 4: 1060. 1904. TYPE: Paraguay. s. loc., Sep. 1898/1899, *E. Hassler* 4489 (holotype, G not seen; isotypes, F [bc] F0074534!, MPU [bc] MPU011503!, NY [bc] NY00138327!, P [bc] P00650864!, P [bc] P00650865!, UC [bc] UC935083!).

Verbena spectabilis Moldenke, Phytologia 2(10): 426. 1948. *Glandularia spectabilis* (Moldenke) Botta, Hickenia 2(28): 128. 1995. TYPE: Argentina. Misiones: Posadas, Loreto, "Magdalena," 6 Feb. 1908, *E. L. Ekman* 1980 (holotype, S [bc] S04-2452!; isotypes, NY [bc] NY00138325!, SI [bc] SI003821!).

Verbena ramboi Moldenke, Phytologia 3(8): 427. 1951. TYPE: Brazil. Rio Grande do Sul: faz. Santa Cecilia pres. S Gabriel, 15 Jan. 1944, *B. Rambo* 25787 (holotype, PACA not seen; isotype, NY [bc] NY00138315!).

Plants suffrutescent, 50–100 cm tall, stems erect or decumbent with ascending floral branches, 4-angled, pubescence hispid, retrorse hairs. Leaves petiolate, petiole 5–7 mm, blade 30–50 × 8–25 mm, entire elliptic to ovate or pinnatilobate, sometimes pinnatisect at apical nodes, apex acute, base acute, margin irregularly serrate, adaxial surface strigose, abaxial surface hispid. Inflorescences arranged in monobotrya or pleiobotrya with frondose paracladia, surpassing the principal inflorescence, inflorescences represented by dense multifloral spikes, enlarged in fruit, peduncles 15–30 mm. Floral bracts 3–5 mm, narrowly ovate, apex acute, strigose, ciliate margin. Calyx 8–10 mm, hispid, teeth acute, 1.8 mm. Corolla 12 mm, externally villous, violet or lilac. Superior pair of stamens with vestigial sessile glandular appendages, surpassing thecae, not surpassing corolla mouth, style 10–11 mm. Cluses 2.8–3.5 mm, apex round.

Distribution and ecology. *Glandularia tomophylla* is found in eastern and central Argentina, Paraguay, and southern Brazil. It grows in rocky fields, forest margins, roadsides, and sandy soils, at elevations between sea level and 650 m.

Notes. *Glandularia tomophylla* has variable leaf morphology, from entire to pinnatilobate, sometimes pinnatisect at the apical nodes (Fig. 31C, C'). This species is similar to *G. peruviana* and *G. tweediana*; however, the latter two are distinguished by longer cluses (4–4.5 mm vs. 2.8–3.5 mm) and unappendaged stamens.

Glandularia tomophylla is also similar to *G. nana* and *G. subincana*; see notes under these two species for further details.

Selected material examined. BRAZIL. **Rio Grande do Sul:** Cachoeira do Sul, *Sobral* 1718 (SI).

31. *Glandularia tweediana* (Niven ex Hook.) P. Peralta, Ann. Missouri Bot. Gard. 98: 400. 2011. Basionym: *Verbena tweediana* Niven ex Hook., Bot. Mag., 63: t. 3541. 1836. *Verbena megapotamica* Spreng. var. *tweediana* (Niven ex Hook.) Kuntze, Revis. Gen. Pl. 3(2): 256. 1898. TYPE: Uruguay. Laguna de La Molina, s.d., *J. Tweedie* s.n. (holotype, K not seen; isotype, SI-76924 fragm. ex K!). Figure 32.

Verbena tweediana Niven ex Hook. var. *arraniana* Niven ex Maund, Botanist 2: tab. 60. 1838. TYPE: *Maund*, Botanist 2: t. 60. 1838 (lectotype, designated by Peralta & Múlgura [2011: 401], tab. 60, in Niven ex Maund, 1838).

Verbena incisa Hook., Bot. Mag. 65: tab. 3628. 1839. *Glandularia incisa* (Hook.) Tronc., Fl. Prov. Buenos Aires, Colecc. Ci. Inst. Nac. Tecnol. Agropecu. 4(5a): 135. 1965. TYPE: Argentina. Santa Fé, s.d., *J. Tweedie* s.n. (holotype, K [bc] K000470715!; isotype, SI-76957, fragm. ex K!).

Verbena megapotamica Spreng. var. *truncatula* Briq., Annuaire Conserv. Jard. Bot. Genève 5–9: 3. 1904. TYPE: Paraguay. s. loc., s.d., *B. Balansa* 1024c (holotype, G not seen).

Verbena tessmannii Moldenke, Phytologia 3: 45. 1948. *Glandularia tessmannii* (Moldenke) P. Peralta & V. Thode, syn. nov. *Rodriguésia* 61(suppl.): 30. 2010. TYPE: Brazil. Paraná, Ponta Grossa, faz. Lagoa Dourada, near Vila Velha, 21 km SE of Ponta Grossa, 830 m.s.m., 17 Feb. 1948, *G. Tessmann* 2923 (holotype, NY [bc] NY00138337!).

Verbena peruviana f. *alba* Moldenke, syn. nov. Phytologia 7: 258. 1960. TYPE: Brazil. Santa Catarina: Sombrio, 10 m, 9 Oct. 1945, *R. Reitz* c1280 (holotype, NY not seen; isotypes, SI [bc] SI004227!, SI [bc] SI004228!).

Prostrate herb, stems decumbent with ascending floral branches, pubescence densely hirsute. Leaves briefly petiolate, petiole 4–7 mm, blade 40–50 × 7–

15 mm, entire, ovate to triangular, apex acute, base truncate, margin lobate or deeply serrate, both surfaces densely hispid. Inflorescences arranged in monobotrya or frondose pleiobotrya, inflorescences represented by dense multifloral spikes, enlarged in fruit, peduncle 25–30 mm. Floral bracts 2.5–6 mm, ovate, apex acute, hirsute-glandular, ciliate margin. Calyx 8–12 mm, densely hispid-glandular, teeth triangular, 0.5 mm. Corolla 14–19 mm, externally villous, lilac or pink, exceptionally white. Superior pair of stamens unappendaged, style 15 mm. Cluses 4–4.5 mm, apex round.

Distribution and ecology. *Glandularia tweedieana* is widely distributed in northern and central Argentina, as well as in Bolivia, Brazil, Paraguay, and Uruguay. It can be found in roadsides, open areas, sandy soils, and forest margins, at elevations between 100 and 2600 m.

Notes. *Glandularia tweedieana* is similar to *G. peruviana*, *G. tomophylla*, and *G. nana*; see differences under these species.

The analyses of the type material of *Verbena tessmannii* and *V. peruviana* f. *alba* demonstrated that both are synonyms of *Glandularia tweedieana*.

Selected material examined. BRAZIL. **Paraná:** Curitiba. Estr. Fed. R. Negro, Km. 9, *Tessmann 1950* (MBM). **Rio Grande do Sul:** Torres, *Reitz 4445* (SI). **Santa Catarina:** Sombiro, 9 Oct. 1945, *Reitz 1281* (SI).

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Appendix 1. List of accepted taxa.

1. *Glandularia angustilobata* (Moldenke) P. Peralta & V. Thode
2. *Glandularia aristigera* (S. Moore) Tronc.
3. *Glandularia balansae* (Briq.) N. O’Leary
4. *Glandularia catharinae* (Moldenke) N. O’Leary & P. Peralta
5. *Glandularia corymbosa* (Ruíz & Pav.) N. O’Leary & P. Peralta
6. *Glandularia dusenii* (Moldenke) N. O’Leary & P. Peralta
7. *Glandularia guaibensis* P. Peralta & V. Thode
8. *Glandularia guaranitica* Tronc.
9. *Glandularia hasslerana* (Briq.) Tronc.

<p>10. <i>Glandularia hatschbachii</i> (Moldenke) N. O’Leary & P. Peralta 11. <i>Glandularia herteri</i> (Moldenke) Tronc. 12. <i>Glandularia humifusa</i> (Cham.) Botta 13. <i>Glandularia jordanensis</i> (Moldenke) N. O’Leary & P. Peralta 14. <i>Glandularia lobata</i> (Vell.) P. Peralta & V. Thode 14a. <i>Glandularia lobata</i> var. <i>lobata</i> 14b. <i>Glandularia lobata</i> var. <i>glabrata</i> (Moldenke) P. Peralta & V. Thode 15. <i>Glandularia marrubiioides</i> (Cham.) Tronc. 16. <i>Glandularia megapotamica</i> (Spreng.) Cabrera & G. Dawson 17. <i>Glandularia nana</i> (Moldenke) Tronc. 18. <i>Glandularia paulensis</i> (Moldenke) A. L. R. Oliveira & Salimena 19. <i>Glandularia peruviana</i> (L.) Small 20. <i>Glandularia phlogiflora</i> (Cham.) Schnack & Covas 21. <i>Glandularia platensis</i> (Spreng.) Schnack & Covas 22. <i>Glandularia rectiloba</i> (Moldenke) P. Peralta & V. Thode 23. <i>Glandularia scrobiculata</i> (Griseb.) Tronc. 24. <i>Glandularia selloii</i> (Spreng.) Tronc. 25. <i>Glandularia sessilis</i> (Cham.) Tronc.</p>	<p>26. <i>Glandularia stellarioides</i> (Cham.) Schnack & Covas 27. <i>Glandularia subincana</i> Tronc. 28. <i>Glandularia tenera</i> (Spreng.) Cabrera 29. <i>Glandularia thymoides</i> (Cham.) N. O’Leary 30. <i>Glandularia tomophylla</i> (Briq.) N. O’Leary & V. Thode 31. <i>Glandularia tweedieana</i> (Niven ex Hook.) P. Peralta</p> <p>Appendix 2. List of newly synonymized taxa.</p> <p><i>Verbena hasslerana</i> Briq. var. <i>glandulosa</i> Moldenke [= <i>Glandularia nana</i> (Moldenke) Tronc.] <i>Verbena peruviana</i> (L.) Britton f. <i>alba</i> Moldenke [= <i>G. tweedieana</i> (Niven ex Hook.) P. Peralta] <i>Verbena pulchra</i> Moldenke [= <i>G. hasslerana</i> (Briq.) Tronc.] <i>Verbena pulchra</i> var. <i>paludicola</i> Moldenke [= <i>G. nana</i> (Moldenke) Tronc.] <i>Verbena tessmannii</i> Moldenke [= <i>G. tweedieana</i> (Niven ex Hook.) P. Peralta] <i>Verbena tristachya</i> Tronc. & Burkart [= <i>G. sessilis</i> (Cham.) Tronc.]</p>
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A BIOGEOGRAPHICAL COMPARISON BETWEEN YUNNAN, SOUTHWEST CHINA, AND TAIWAN, SOUTHEAST CHINA, WITH IMPLICATIONS FOR THE EVOLUTIONARY HISTORY OF THE EAST ASIAN FLORA¹

*Hua Zhu*²

ABSTRACT

Located in southwestern and southeastern China, respectively, Yunnan and Taiwan are of biogeographical significance for the floristic diversity and evolution of the East Asian flora. A total of 13,253 seed plant species in 2140 genera and 225 families are recognized from Yunnan, while 3411 species in 1234 genera and 190 families are recognized from Taiwan. Although the flora of Yunnan is much more diverse than the flora of Taiwan, it is conspicuously similar in floristic composition and biogeographical elements. Yunnan and Taiwan share many of the same species-rich families in their floras. In both areas, families of tropical distribution contribute 52.4% and 50.5% of the total families in Yunnan and Taiwan, respectively, and the genera of tropical distribution contribute 57.3% of the flora in Yunnan and 60.9% of the flora in Taiwan. Yunnan and Taiwan have floristic similarities of 96.3% at the family level and 84.7% at the generic level. These similarities indicate that Yunnan and Taiwan have close floristic affinities. However, the floras of Yunnan and Taiwan have diverged to some extent. Yunnan has eight East Asian families and two Chinese endemic families, of which only two East Asian families are shared with Taiwan. Of the 12 tropical Asian families in Yunnan, 10 are not seen in Taiwan. Compared to Taiwan, Yunnan has 474 genera of tropical Asian distribution, which contribute 22.1% of its total genera, while Taiwan has 165 genera of tropical Asian distribution, contributing only 13.4% of its total genera. Furthermore, the patterns of geographical elements indicate that genera with transcontinental distributions, such as pantropic, Old World tropic, north temperate, or East Asia and North America disjunctions, are more likely to be shared by Yunnan and Taiwan, while those genera with distributions of tropical Asia, Old World temperate, temperate Asia, Mediterranean and western to central Asia, East Asia, and Chinese endemic are more often represented only in Yunnan. The flora of Yunnan might be derived from a Tertiary subtropical East Asian flora and has been diversified in its biogeographical elements following tectonic events since the Late Tertiary: northwestern Yunnan has evolved a temperate-featured flora with the uplift of the Himalayas, and southern Yunnan has evolved a tropical Asian flora with extrusion of the Indochina block. The flora of Taiwan could mainly derive from the East Asian flora with uplifting to an island after the Late Tertiary, and could have a relatively unsophisticated evolutionary history compared to Yunnan.

Key words: Biogeography, China, East Asian flora, floristics, Taiwan, Yunnan.

In his floristic regionalization of the world, Takhtajan (1978) delineated the Eastern Asiatic floristic region. Later, Wu and Wu (1996) raised this floristic region to kingdom level, the Eastern Asiatic Kingdom, considering its uniqueness with more than 30 endemic families and an exceptionally large number of endemic genera. The Eastern Asiatic Kingdom was further divided into Sino-Himalayan (with 144 endemic genera) and Sino-Japanese (with 104 endemic genera) subkingdoms (Wu & Wu, 1996). The Eastern Asiatic Kingdom was supposed to be one of the major centers for the evolution of higher seed plants, as the floristic

kingdom is especially rich in gymnosperms and primitive angiosperms (Wu & Wu, 1996). It is important for botanists who study the history of the temperate floras of the Northern Hemisphere and the tropical flora of southeastern Asia to deeply understand Eastern Asiatic flora. Yunnan and Taiwan comprise the southwestern and southeastern wings, respectively, of the Eastern Asiatic floristic region (Takhtajan, 1978), although their southernmost parts were in the northern margin of the Paleotropical kingdom, and Taiwan, as a whole, was later moved to the Paleotropical kingdom by Wu and Wu (1996). Yunnan and Taiwan are of

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important biogeographical significance for the East Asian flora; they are at similar latitudes and have similar geography and vegetation. Comparing their floras may lead to a better understanding of the geological history, floristic variation, and evolution of East Asian floras.

The flora of Yunnan was primarily studied by Li and Walker (1986). Further research revealed that southern Yunnan has a tropical flora of Malaysian affinity (Zhu, 1997, 2008a; Zhu & Yan, 2009); central Yunnan is largely characterized by a subtropical East Asian flora (Yan et al., 2009), while northwestern Yunnan has a temperate Himalayan flora (Zhu, 2015). Floristic relationships between Taiwan and mainland China have been discussed previously (Ying & Hsu, 2002), and paleobotanical comparisons between Taiwan and mainland China have also been made (Song & Huang, 2004). These studies have shown that both the present flora and the palynoflora of Taiwan have close affinities to those of mainland China. It has also been observed that some taxa in Taiwan are related to taxa from southwestern China and the Himalayas, e.g., *Taiwania* Hayata, which is disjunctively distributed in northern Myanmar, the Hengduan Mountains of Yunnan, Hubei in central China, and Taiwan (Yu, 1995). Ying and Hsu (2002) recorded 15 genera of seed plants in Taiwan with Chinese-Himalayan distributions. While it has been observed that the gymnosperms of Taiwan have a closer affinity to southwestern China than to southeastern Asia (Ying & Hsu, 2002), the floristic relationships between southwestern China and Taiwan are understudied.

In this article, I compare the floras of Yunnan and Taiwan and their biogeographical affinities, to contribute to our understanding of geological history and the floristic evolution and variation of East Asia.

GEOGRAPHY

Yunnan Province is in southwestern China between 21°09' to 29°15'N and 97°32' to 106°12'E and occupies an area of 394,100 km². It has a mountainous topography with mountain ridges generally running in a north-south direction, decreasing in elevation southward from 6740 m at the highest mountain summit in the northwest to 76.4 m at the lowest valley bottom in the southeast (Red River). The general climatic pattern is: (1) tropical wet climates in the southern lowlands, (2) tropical dry climates in deep valleys below 1000 m, due to the foehn effect, (3) subtropical climates on the central plateau, and (4) temperate to cold temperate climates in the northern high mountains. It has a roughly annual precipitation of less than 1000 mm in the

northern mountains, 1000–1250 mm on the central plateau, and 1250–2250 mm in the south except in the deep dry valleys. Yunnan is a region with tropical areas at the horizontal base because almost all areas of lower elevation are tropical in nature regardless of their latitudinal location (Zhu, 2008b).

Taiwan is in southeastern China, at similar latitudes to Yunnan. It is a large (35,989 km²) continental island and lies between 21°45' to 25°56'N and 119°18' to 124°34'E. It also has a mountainous topography with mountain ridges in the center, running in a north-south direction. Its elevation ranges from sea level to 3997 m on the highest mountain summit in Yushan (Huang, 1993). Taiwan shows a transition from a tropical monsoon climate with an annual temperature of 23°–24°C in the south to a southern subtropical climate with an annual temperature of ca. 21°C in the north. It has an annual precipitation that exceeds 1500 mm across the island. Taiwan is also a region with tropical areas at its horizontal base.

VEGETATION

Yunnan supports a rich biodiversity and various vegetation types, making it a key area in biogeography and a hotspot for biodiversity (Myers, 1998). The vegetation types of Yunnan include tropical rainforest, subtropical evergreen broad-leaved forest, warm-temperate deciduous broad-leaved forest, temperate coniferous and broad-leaved mixed forest, cold temperate coniferous forest, alpine shrubs and meadows, as well as thorny shrubs and savanna in dry-hot valleys (Wu, 1987). The variety in these vegetation types shows a more or less mosaic distribution pattern, which occurs in response to the extremely diverse topography in Yunnan. It is conspicuous that the vegetation distribution of Yunnan corresponds more to elevation than latitude (Zhu, 2008b).

Taiwan has very similar vegetation types to those of Yunnan. It has tropical rainforest and monsoon forest in the lowlands; subtropical evergreen broad-leaved forest, which is the main vegetation type in Taiwan, in the lower montane zone; temperate coniferous–broad-leaved mixed forest and evergreen-deciduous mixed forest in the upper montane zone; and cold temperate *Picea* A. Dietr.–*Abies* Mill. forest at altitudes above 3000 m (Huang, 1993; Song & Xu, 2003).

MATERIALS AND METHODS

In the *Flora of Taiwan* (Huang & Editorial Committee of the Flora of Taiwan, 1994), which incorporated the newest checklist of vascular plants

of Taiwan (Boufford et al., 2003), excluding cultivated, introduced, and invasive species, and rectifying the circumscription of families that followed APG III (Chase & Reveal, 2009; APG III, 2009), and species following the nomenclature and classification as presented in Tropicos® of the Missouri Botanical Garden (<http://www.tropicos.org>), an updated list of native seed plants in Taiwan was completed, with a total of 3411 species in 1234 genera and 190 families. A similar circumscription of families and species was obtained, using the *Flora of Yunnan* (Wu, 1977–2006) and Tropicos®, with a total of 13,253 native seed plant species in 2140 genera and 225 families. Complete lists of families and genera with species numbers for Yunnan and Taiwan are given in Appendix 1. Floristic and geographical attributes of the floras of Yunnan and Taiwan were then analyzed. Patterns of seed plant distribution of these floras were quantified at the generic level based on documentation from Wu (1991) and Wu et al. (2006) and at the family level according to Wu et al. (2003). Comparisons of both floristic composition and geographical elements were made to assess the floristic similarity and variation as well as biogeographical affinities between these two regions.

RESULTS

FLORISTIC COMPOSITION OF THE FLORAS IN YUNNAN AND TAIWAN

A total of 13,253 native seed plant species in 2140 genera and 225 families were recognized from Yunnan. The families with high species richness include Poaceae (874 species), Asteraceae (787), Orchidaceae (774), Fabaceae (637), Rosaceae (460), Lamiaceae (446), Rubiaceae (365), Ericaceae (360), Ranunculaceae (310), Cyperaceae (273), Umbelliferae (250), Euphorbiaceae (226), Primulaceae (221), Lauraceae (205), and Gentianaceae (202). A total of 3411 species in 1234 genera and 190 families were recognized from Taiwan. Similar to the flora of Yunnan, the families with high species richness in Taiwan include Orchidaceae (334 species), Poaceae (317), Asteraceae (204), Fabaceae (195), Cyperaceae (159), Lamiaceae (103), Rubiaceae (97), Rosaceae (90), Euphorbiaceae (78), Urticaceae (61), and Lauraceae (57). The total number of native seed plant species in Yunnan is more than four times the total species in Taiwan.

The top 50 families ranking in species richness from both Yunnan and Taiwan are compared in Table 1. The dominant 50 families in Yunnan include a total of 10,447 species, contributing to 78.8% of its total flora (13,253 species), while the

dominant 50 families in Taiwan have a total of 2696 species, contributing to 79.0% of the total flora (3411 species). The floras of Yunnan and Taiwan are conspicuously similar in their species-rich families. Thirty-nine of the dominant 50 families in Yunnan are shared by Taiwan. The other 11 dominant families in Yunnan are Balsaminaceae, Begoniaceae, Berberidaceae, Campanulaceae, Fumariaceae, Gesneriaceae, Orobanchaceae, Primulaceae, Salicaceae, Sapindaceae, and Saxifragaceae; most of them are species-rich families in the Himalayas, while Gesneriaceae has high species diversity in southwestern China, especially in limestone habitats.

GEOGRAPHICAL ELEMENTS

Geographical elements of the floras of Yunnan and Taiwan at the family level are enumerated in Table 2. Families with tropical distribution dominate both, contributing to 52.4% and 50.5% of the total families in Yunnan and Taiwan, respectively, with those of pantropical distribution (e.g., Acanthaceae, Anacardiaceae, Annonaceae, Apocynaceae, Araceae, Arecaceae, Clusiaceae, Combretaceae, Icacinaceae, Myristicaceae, and Sapotaceae), making up 34.2% in Yunnan and 37.9% in Taiwan. Excluding cosmopolitan families with little geographical significance, those of north temperate distribution (e.g., Adoxaceae, Betulaceae, Caprifoliaceae, Cornaceae, Fagaceae, Fumariaceae, Hamamelidaceae, Orobanchaceae, and Salicaceae) rank second, contributing to 12.4% and 14.2% of their total floras, respectively. The flora of Yunnan includes 12 families of tropical Asian distribution (e.g., Crypteroniaceae, Escalloniaceae, Ixonanthaceae, Pentaphragmataceae, Pentaphylacaceae, Rafflesiaceae, Sabiaceae, and Sladeniaceae), eight families of East Asian distribution (e.g., Cercidiphyllaceae, Circaeasteraceae, Dipentodontaceae, Eupteleaceae, Stachyuraceae, and Tetracentraceae), and two families endemic to China (Eucommiaceae and Ginkgoaceae). The flora of Taiwan, in contrast, includes only two tropical Asian families (Akanthaceae, Sabiaceae), three East Asian families (Cephalotaxaceae, Stachyuraceae, and Trochodendraceae), and no Chinese endemic families.

Geographical elements at the generic level are enumerated in Table 3. The genera of tropical distribution contribute to 57.3% of the flora of Yunnan and 60.9% of the flora of Taiwan. The genera of tropical Asian distribution make up the highest proportion of the total genera of Yunnan (22.1%), while the genera of pantropical distribution constitute the highest proportion of the total genera of

Table 1. Dominant 50 families with high species richness among the floras of Yunnan (making up a total of 10,447 species, 78.8% of the total flora) and Taiwan (making up a total of 2696 species, 79.0% of the total flora).

Flora of Yunnan			Flora of Taiwan		
Family	No. of species	Species (%)	Family	No. of species	Species (%)
Poaceae	874	6.6	Orchidaceae	334	9.8
Asteraceae	787	5.9	Poaceae	317	9.3
Orchidaceae	774	5.8	Asteraceae	204	6.0
Fabaceae	637	4.8	Fabaceae	195	5.7
Rosaceae	460	3.5	Cyperaceae	159	4.7
Lamiaceae	446	3.4	Lamiaceae	103	3.0
Rubiaceae	365	2.8	Rubiaceae	97	2.8
Ericaceae	360	2.7	Rosaceae	91	2.7
Ranunculaceae	310	2.3	Euphorbiaceae	78	2.3
Cyperaceae	273	2.1	Urticaceae	61	1.8
Umbelliferae	250	1.9	Lauraceae	57	1.7
Euphorbiaceae	226	1.7	Fagaceae	48	1.4
Primulaceae	221	1.7	Convolvulaceae	44	1.3
Lauraceae	205	1.5	Polygonaceae	42	1.2
Gentianaceae	202	1.5	Ranunculaceae	38	1.1
Gesneriaceae	194	1.5	Ericaceae	36	1.1
Apocynaceae	192	1.4	Araceae	33	1.0
Urticaceae	190	1.4	Umbelliferae	33	1.0
Liliaceae	181	1.4	Theaceae	32	0.9
Acanthaceae	175	1.3	Acanthaceae	31	0.9
Orobanchaceae	161	1.2	Apocynaceae	31	0.9
Saxifragaceae	145	1.1	Moraceae	31	0.9
Fagaceae	142	1.1	Rutaceae	31	0.9
Caryophyllaceae	139	1.0	Liliaceae	30	0.9
Zingiberaceae	139	1.0	Plantaginaceae	29	0.9
Celastraceae	126	1.0	Cruciferae	28	0.8
Theaceae	120	0.9	Symplocaceae	26	0.8
Araliaceae	117	0.9	Caryophyllaceae	25	0.7
Berberidaceae	116	0.9	Solanaceae	25	0.7
Cruciferae	115	0.9	Boraginaceae	23	0.7
Balsaminaceae	112	0.8	Gentianaceae	23	0.7
Salicaceae	111	0.8	Malvaceae	23	0.7
Polygonaceae	108	0.8	Cucurbitaceae	22	0.6
Moraceae	103	0.8	Aquifoliaceae	21	0.6
Rutaceae	102	0.8	Smilacaceae	21	0.6
Araceae	99	0.7	Celastraceae	20	0.6
Cucurbitaceae	99	0.7	Myrsinaceae	20	0.6
Vitaceae	96	0.7	Commelinaceae	19	0.6
Rhamnaceae	93	0.7	Crassulaceae	19	0.6
Begoniaceae	92	0.7	Linderniaceae	19	0.6
Oleaceae	90	0.7	Oleaceae	19	0.6
Campanulaceae	85	0.6	Vitaceae	19	0.6
Caprifoliaceae	84	0.6	Zingiberaceae	19	0.6
Sapindaceae	81	0.6	Caprifoliaceae	18	0.5
Aquifoliaceae	79	0.6	Hydrocharitaceae	18	0.5
Fumariaceae	79	0.6	Amaranthaceae	17	0.5
Convolvulaceae	74	0.6	Loranthaceae	17	0.5
Crassulaceae	74	0.6	Melastomataceae	17	0.5
Melastomataceae	73	0.6	Rhamnaceae	17	0.5
Boraginaceae	71	0.5	Araliaceae	16	0.5

Table 2. Biogeographical elements of seed plants at the family level in the floras of Yunnan (Southwest China) and Taiwan (Southeast China).

Biogeographical elements at family level	Yunnan		Taiwan	
	No. of families	%*	No. of families	%*
Cosmopolitan	58	25.8	58	30.5
Pantropic	77	34.2	72	37.9
Tropical Asia and tropical America disjunct	16	7.1	12	6.3
Old World tropic	5	2.2	4	2.1
Tropical Asia to tropical Australia	6	2.7	5	2.6
Tropical Asia to tropical Africa	2	0.9	1	0.5
Tropical Asia	12	5.3	2	1.1
North temperate	28	12.4	27	14.2
East Asia and North America disjunct	10	4.4	4	2.1
Old World temperate	1	0.4	2	1.1
Temperate Asia	0	0.0	0	0.0
Mediterranean, Western Asia to Central Asia	0	0.0	0	0.0
Central Asia	0	0.0	0	0.0
East Asia	8	3.6	3	1.6
Endemic to China	2	0.9	0	0.0
Total no. of families	225	100.0	190	100.0

* Percentages are calculated by the number of families in each geographical element divided by the total number of families in all geographical elements, then multiplied by 100%.

Taiwan (21.6%). In the flora of Yunnan, the genera of pantropical distribution constitute 14.4% of the total genera, followed by north temperate (10.9%) and East Asia (9.9%). In the flora of Taiwan, the genera of tropical Asian distribution contribute 13.4% of the total genera, followed by north temperate (12.3%). The genera endemic to China contribute 5.4% (115 genera) of the total flora of Yunnan but only 1.5% (18 genera) of the total flora of Taiwan.

FLORISTIC SIMILARITY BETWEEN THE FLORAS OF YUNNAN AND TAIWAN

Similarity coefficients between the floras of Yunnan and Taiwan at the family and generic levels are given in Table 4. They are 96.3% at the family level and 84.7% at the generic level. Among 190 families of seed plants in Taiwan, only seven families are not known from Yunnan: Flagellariaceae, Good-

Table 3. Biogeographical elements of seed plant taxa at the generic level in the floras of Yunnan (Southwest China) and Taiwan (Southeast China).

Biogeographical elements at generic level	Yunnan		Taiwan	
	No. of genera	%*	No. of genera	%*
Cosmopolitan	90	4.2	88	7.1
Pantropic	309	14.4	267	21.6
Tropical Asia and tropical America disjunct	45	2.1	34	2.8
Old World tropic	146	6.8	117	9.5
Tropical Asia to tropical Australia	146	6.8	115	9.3
Tropical Asia to tropical Africa	109	5.1	53	4.3
Tropical Asia	474	22.1	165	13.4
North temperate	234	10.9	152	12.3
East Asia and North America disjunct	89	4.2	62	5.0
Old World temperate	111	5.2	50	4.1
Temperate Asia	21	1.0	6	0.5
Mediterranean, Western Asia to Central Asia	23	1.1	7	0.6
Central Asia	17	0.8	0	0.0
East Asia	211	9.9	100	8.1
Endemic to China	115	5.4	18	1.5
Total no. of genera	2140	100.0	1234	100.0

* Percentage was calculated by the number of genera in each geographical element divided by the number of genera of all geographical elements, then multiplied by 100%.

Table 4. Similarity coefficients at the family and genus levels between the floras of Yunnan (225 families, 2140 genera) and Taiwan (190 families, 1234 genera).

Floristic similarities	Shared no./Similarity coefficients
At family level	183/96.3*
At generic level	1045/84.7*

* The similarity coefficient between A and B is calculated by the number of taxa shared by both A and B divided by the lowest number of taxa of A or B, then multiplied by 100%.

eniaceae, Phylodraceae, Ruppiaceae, Triuridaceae, Trochodendraceae, and Zosteraceae. Except for Trochodendraceae, which is distributed in Taiwan, the Ryukyu Islands, and Japan, the other six families are mostly seashore, wetland, or water plants and occur in southeast mainland China.

Among 225 families of seed plants in Yunnan, 43 families are not known from Taiwan (Table 5). They include 10 tropical Asian families, seven pantropical families, five North temperate families, six East Asian families, and two Chinese endemic families.

There are 1045 genera of native seed plants shared by Yunnan and Taiwan. However, 1095 genera in Yunnan are not known from Taiwan, while 190 genera in Taiwan are not known from Yunnan (Table 6). Of these shared genera, the pantropical elements contribute 23.2%, north temperate 13.4%, and tropical Asia 12.3%. Of those genera only in Yunnan, 343 genera are of tropical Asian distribution (31.3%), 138 genera are of East Asian distribution (12.6%), 106 are endemic to China (9.7%), and 94 genera are of north temperate distribution (8.6%). Of the genera only in Taiwan, those of tropical Asian distribution contribute 19.0%, those of tropical Asian to tropical Australian distribution contribute 14.8%, those of pantropical distribution contribute 13.2%, and those of East Asian distribution contribute 14.3%.

DISCUSSION

Yunnan and Taiwan are at similar latitudes and have a similar geography, although they are located at opposite ends of the Eastern Asiatic floristic region. They are conspicuously similar in floristic composition and geographical elements. They have higher similarities at the family and generic levels than usually expected. Although the flora of Yunnan is much more diverse in species than is the flora of Taiwan, the following similarities between them are revealed. (1) The top 50 families ranking in species richness in Yunnan and Taiwan contribute to 78.8% and 79.0% of their total floras, respectively. Thirty-nine of the top 50 families in both Yunnan and Taiwan are shared between the two provinces. (2) The

families of tropical distribution make up 52.4% and 50.5% of the total families in Yunnan and Taiwan, respectively, of which those of pantropical distribution contribute most among all geographical elements, making up 34.2% of the total families in Yunnan and 37.9% of the total families in Taiwan. The genera of tropical distribution contribute 57.3% of the flora of Yunnan and 60.9% of the flora of Taiwan. (3) The flora of Taiwan shares 96.3% of its families and 84.7% of its genera with the flora of Yunnan. The high floristic similarities between Yunnan and Taiwan indicate their close floristic affinities, despite the distance between the provinces.

The close floristic affinities cannot be explained only by the similar latitudes and geography of the provinces, but also by the geological history of East Asia and the Himalayas. It has been suggested that Taiwan was uplifted to an island after the Late Tertiary (Teng, 1990; Huang et al., 2001; Song & Huang, 2004), synchronous with the uplift of the Himalayas (Shi et al., 1998, 1999). During the formation of Taiwan, there were intermittent land connections to mainland China until the Late Holocene. The geological history of Taiwan might explain the close floristic affinity to Yunnan. Among the genera of East Asia distribution in Taiwan, Ying and Hsu (2002) mentioned that 15 genera were typical Sino-Himalayan distribution. Evidently, the floristic connection between Yunnan and Taiwan can be attributed to the success of the uplift of the Himalayas, which controlled their formations during the same geological time.

Table 7 shows the floristic similarities at the family and genus levels between the floras of Yunnan, Guangxi (Qin & Liu, 2010), Guangdong (Ye & Xing, 2005), Fujian, and Taiwan Provinces in southern China, which indicate that the floristic similarities between these provinces are high (more than 92.6% at the family level and 73.3% at the genus level), and their floras are in a continuous transition.

The high floristic similarity between these compared provinces makes it reasonable that main parts of Yunnan and Taiwan were included in the East Asian floristic region by Takhtajan (1978). There are eight families of East Asian distribution, Cephalotaxaceae, Cercidiphyllaceae, Circaeasteraceae, Dipentodontaceae, Eupteleaceae, Stachyuraceae, Tetracentraceae, and Toricelliaceae, and 211 genera of East Asian distribution in Yunnan. There are three families of East Asian distribution, i.e., Cephalotaxaceae, Stachyuraceae, and Trochodendraceae, and 100 genera of East Asian distribution in Taiwan. However, of the eight families of East Asian distribution in Yunnan, only two families are

Table 5. Seed plant families found in Yunnan but not in Taiwan (43 families). The number of species and genera are included as well as their biogeographical distribution types.

Family	Number of genera	Number of species	Distribution types
Borthwickiaceae	1	1	tropical Asia
Burseraceae	3	13	pantropic
Butomaceae	2	2	north temperate
Calycanthaceae	1	2	East Asia and North America disjunct
Carlemanniaceae	2	2	tropical Asia
Cercidiphyllaceae	1	1	Sino-Japan
Circaeasteraceae	1	1	Sino-Himalaya
Cletheraceae	1	5	tropical Asia and tropical America disjunct
Crypteroniaceae	1	1	tropical Asia
Dilleniaceae	2	4	pantropic
Dipentodontaceae	1	1	Sino-Himalaya
Dipterocarpaceae	5	7	pantropic
Ephedraceae	1	1	North temperate
Erythroxylaceae	1	2	pantropic
Escalloniaceae	1	1	tropical Asia
Eucommiaceae	1	1	endemic to China
Eupteleaceae	1	1	East Asia
Ginkgoaceae	1	1	endemic to China
Gnetaceae	1	4	pantropic
Hippocastanaceae	1	6	tropical Asia and tropical America disjunct
Ixonanthaceae	1	2	tropical Asia
Juncaginaceae	1	2	cosmopolitan
Linaceae	4	6	North temperate
Martyniaceae	1	1	tropical Asia and tropical America disjunct
Menyanthaceae	2	3	cosmopolitan
Myristicaceae	3	10	pantropic
Nyssaceae	2	5	East Asia and North America disjunct
Paeoniaceae	1	5	North temperate
Pandaceae	1	1	tropical Asia to tropical Africa
Pedaliaceae	1	1	Old World tropic
Pentaphragmataceae	1	1	tropical Asia
Pentaphylacaceae	1	1	tropical Asia
Podostemaceae	1	1	tropical Asia and tropical America disjunct
Polemoniaceae	1	1	North temperate
Rafflesiaceae	1	1	tropical Asia
Sargentodoxaceae	1	1	tropical Asia
Sladeniaceae	1	1	tropical Asia
Sonneratiaceae	1	1	Old World tropic
Stylidiaceae	1	1	pantropic
Tamaricaceae	2	4	Old World temperate

Table 5. Continued.

Family	Number of genera	Number of species	Distribution types
Tetracentraceae	1	1	Sino-Himalaya
Tetramelaceae	1	1	tropical Asia to tropical Australia
Toricelliaceae	1	1	Sino-Himalaya

shared with Taiwan. None of the two Chinese endemic families in Yunnan (Eucommiaceae and Ginkgoaceae) occurs in Taiwan. Although there are 73 genera of East Asian distribution common to Yunnan and Taiwan, there are another 138 East Asian genera found in Yunnan alone and 27 East Asian genera found in Taiwan alone. Similarly, there are 10 genera endemic to China that are common in Yunnan and Taiwan, while 106 Chinese endemic genera are found in Yunnan alone and eight Chinese endemic genera are found in Taiwan alone. These numbers indicate that Yunnan and Taiwan, although located at opposite ends of the Eastern Asiatic floristic region, have diverged to some extent. The flora of Yunnan has been diversified in its biogeographical elements, while the flora of Taiwan seems to have had a relatively unsophisticated evolutionary history.

The floristic similarities at the family and genus levels between these provinces in southern China (Table 7) indicate that the lowest similarities are between Fujian and adjacent Taiwan. Dipterocarpaceae fossils were found in the Middle Miocene at 24°12'N, 117°53'E in Fujian (Shi & Li, 2010) but have not been recorded in Taiwan. This may imply that the flora of Taiwan significantly evolved after the Miocene. Ying and Hsu (2002) mentioned that endemic species contribute 29.3% in Taiwan, but only four genera are endemic. If compared with Ceylon, an island of continental origin in tropical Asia, which has 27 endemic genera and 853 endemic species among its 1056 genera and 2855 angiosperm plants (Gunatilleke & Gunatilleke, 1990), the much lower endemism at the generic level in Taiwan may imply that it was not isolated biogeographically from mainland China by the Taiwan Strait until relatively recently.

In the flora of Yunnan, the genera of tropical Asian distribution contribute the highest proportion of the total genera at 22.1%, and those of pantropical distribution contribute 14.4%. In the flora of Taiwan, the genera of pantropical distribution contribute the highest proportion of the total genera at 21.6%, and those of tropical Asian distribution contribute 13.4%.

Table 6. Biogeographical elements at the generic level for genera shared by Yunnan and Taiwan and for genera found in only one of the two provinces.

Biogeographical elements at generic level	Shared by Yunnan and Taiwan		Found in Yunnan, SW China		Found in Taiwan, SE China	
	No. of genera	%*	No. of genera	%*	No. of genera	%*
Cosmopolitan	80	7.7	10	0.9	8	4.2
Pantropic	242	23.2	67	6.1	25	13.2
Tropical Asia and tropical America disjunct	28	2.7	17	1.6	6	3.2
Old World tropic	100	9.6	46	4.2	17	9.0
Tropical Asia to tropical Australia	87	8.3	59	5.4	28	14.8
Tropical Asia to tropical Africa	48	4.6	61	5.6	5	2.6
Tropical Asia	129	12.3	343	31.3	36	19.0
North temperate	140	13.4	94	8.6	12	6.3
East Asia and North America disjunct	54	5.2	36	3.3	8	4.2
Old World temperate	47	4.5	64	5.8	3	1.6
Temperate Asia	6	0.6	15	1.4	0	0.0
Mediterranean, Western Asia to Central Asia	1	0.1	22	2.0	6	3.2
Central Asia	0	0.0	17	1.6	0	0.0
East Asia	73	7.0	138	12.6	27	14.3
Endemic to China	10	1.0	106	9.7	8	4.2
Total no. of genera	1045	100.0	1095	100.0	190	100.0

*Percentage was calculated by the number of genera in each geographical element divided by the number of genera of all geographical elements, then multiplied by 100%.

The relatively high proportion of the tropical Asian element in Yunnan supports the tectonic hypothesis that the uplift in the Himalaya-Tibetan plateau region, resulting from crustal thickening and lateral extrusion of Indochina, occurred synchronously during the transition between the Oligocene and Miocene as a reaction to the Indo-Asian collision (Tapponnier et al., 1990; Che et al., 2010). It is apparent that the flora of Yunnan was strongly affected by the tropical Asian flora in its late evolution (Zhu, 2012).

Of the 474 genera of tropical Asian distribution in Yunnan, only 129 are shared with Taiwan (Table 6). Of the 12 tropical Asian families in Yunnan, 10 are not seen in Taiwan (Table 5). There are some pantropical families in Yunnan, such as Burseraceae, Dipterocarpaceae, Dilleniaceae, and Myristicaceae, which are well-diversified woody families in the tropical Asian rainforest, not found in Taiwan, with the exception of Myristicaceae, which is only naturally found in Lanyu Island, off of southwestern Taiwan. Obviously, these tropical Asian elements

Table 7. Similarity coefficients at the family and genus levels between the floras of Yunnan (225 families, 2140 genera), Guangxi (209 families, 1653 genera), Guangdong (197 families, 1413 genera), Fujian (193 families, 1155 genera), and Taiwan (190 families, 1234 genera).

Compared flora	Yunnan	Guangxi	Guangdong	Fujian	Taiwan
Similarity coefficients at family level*					
Yunnan	100				
Guangxi	93.3	100			
Guangdong	94.2	99.0	100		
Fujian	96.4	96.4	93.3	100	
Taiwan	95.8	95.8	93.2	92.6	100
Similarity coefficients at generic level*					
Yunnan	100				
Guangxi	87.4	100			
Guangdong	86.3	91.0	100		
Fujian	88.4	90.4	87.5	100	
Taiwan	84.6	78.2	75.0	73.3	100

* The similarity coefficient between A and B is calculated by the number of taxa shared by both A and B divided by the lowest number of taxa of A or B, then multiplied by 100%.

have been developed in Yunnan since the Late Tertiary, but they are not a major contribution to the flora of Taiwan. The pollen record from the Toushe Basin (23°49'N; 120°53'E; 650 m above sea level) in central Taiwan displayed that instead of today's closed subtropical evergreen broad-leaved forest dominated by *Machilus* Rumph.–*Castanopsis* (D. Don) Spach surrounding the basin, temperate deciduous forest predominated during most of the last glacial interval (Liew et al., 2006). This infers that Taiwan had a much colder climate in the past, which may be the reason that tropical plants of Southeast Asia have not been a major floristic element in Taiwan. In their floristic regionalization of China, Wu and Wu (1996) and Wu et al. (2010) moved Taiwan into the Paleotropical floristic kingdom. Based on the information above, it is better to keep Taiwan under the Eastern Asiatic Kingdom.

Looking across geographical elements at the shared genera, and the genera only in Yunnan or Taiwan (Table 6), the geographical elements can be divided into two groups. In one group, there are more shared than unshared genera, including cosmopolitan, pantropical, tropical Asia and tropical America disjunct, Old World tropic, north temperate, and East Asia and North America disjunct distributions. These geographical elements have a predominantly transcontinental distribution, although some of them could be easily dispersed ones. The second group has more unshared than shared genera, found in Yunnan, including those elements of tropical Asia, tropical Asia to tropical Africa, Old World temperate, temperate Asia, Mediterranean and western to central Asia, central Asia, East Asia, and Chinese endemic distributions. The occurrences of the genera of these distributions in Yunnan can be attributed to tectonic events, such as the collision of the Indian plate of Gondwana, the Tethys ocean closure, the Himalayan uplift, and extrusion of the Indochina block. From these patterns of geographical elements in Yunnan and Taiwan, one could infer that the floras of Yunnan and Taiwan are both derived from a common Tertiary flora of East Asia, composed mainly of elements with pantropic, Old World tropic, north temperate, and East Asia and North America disjunct distributions, and later diverged largely by the additions of tropical Asia, tropical Asia to tropical Africa, Old World temperate, East Asia, and Chinese endemic elements in Yunnan after tectonic events since the Late Tertiary. As a result, vegetation in northwestern Yunnan has evolved into a temperate-featured flora corresponding with the uplift of the Himalayas, while the vegetation in southern Yunnan has evolved a

more tropical Asian flora with the extrusion of the Indochina block. The flora of Taiwan underwent a relatively unsophisticated evolutionary history with uplifting to an island after the Late Tertiary.

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- Appendix 1. Families and genera of seed plants known for Yunnan (Y) and Taiwan (T). Note the sources that support the lists from the *Flora of Yunnan* (Wu, 1977–2006, and updated database at KUN) and the *Flora of Taiwan* (Boufford et al., 2003)
- Acanthaceae** (Y, gen. 55; T, gen. 14): *Acanthus* L. (Y, sp. 1); *Adenacanthus* Nees (Y, sp. 1), *Adhatoda* Mill. (Y, sp. 1), *Aechmanthera* Nees (Y, spp. 2), *Andrographis* Wall. (Y, spp. 2), *Asystasia* Blume (Y, spp. 3), *Asystasiella* Lindau (Y, sp. 1; T, sp. 1), *Avicennia* L. (T, sp. 1), *Baphicacanthus* Bremek. (Y, sp. 1), *Barleria* L. (Y, spp. 3), *Calophanoides* Ridl. (Y, spp. 11), *Championella* Bremek. (Y, spp. 3), *Chroesthes* Benoist (Y, sp. 1), *Clinacanthus* Nees (Y, sp. 1), *Codonacanthus* Nees (Y, sp. 1; T, sp. 1), *Cystacanthus* T. Anderson (Y, spp. 4), *Dicliptera* Juss. (Y, spp. 5; T, sp. 1), *Diflugossa* Bremek. (Y, spp. 4), *Dipteracanthus* Nees (Y, sp. 1; T, sp. 1), *Echinacanthus* Nees (Y, sp. 1), *Eranthemum* L. (Y, spp. 4), *Gendarussa* Nees (Y, spp. 2), *Goldfussia* Nees (Y, spp. 7), *Gutzlaffia* Hance (Y, sp. 1), *Hemigraphis* Nees (T, spp. 3), *Hygrophila* R. Br. (Y, spp. 4; T, spp. 4), *Hymenochlaena* Bremek. (Y, sp. 1), *Hypoestes* Sol. ex R. Br. (Y, sp. 1; T, spp. 2), *Isoglossa* Oerst. (Y, sp. 1), *Kudoacanthus* Hosok. (T, sp. 1), *Lepidagathis* Willd. (Y, spp. 2; T, spp. 4), *Mananthes* Bremek. (Y, spp. 4), *Nelsonia* R. Br. (Y, sp. 1), *Ophiorrhizophyllon* Kurz (Y, sp. 1), *Paragutzlaffia* H. P. Tsui (Y, spp. 2), *Pararuellia* Bremek. & Nannenga-Bremek. (Y, spp. 3), *Perilepta* Bremek. (Y, spp. 3), *Peristrophe* Nees (Y, spp. 7; T, spp. 2), *Phaulopsis* Willd. (Y, sp. 1), *Phlogacanthus* Nees (Y, spp. 4), *Pseudaechmanthera* Bremek. (Y, sp. 1), *Pseuderanthemum* Radlk. (Y, spp. 7), *Pteracanthus* (Nees) Bremek. (Y, spp. 24), *Pteroptychia* Bremek. (Y, sp. 1), *Pyrrothrix* Bremek. (Y, spp. 3), *Rhaphidospora* Nees (Y, sp. 1), *Rhinacanthus* Nees (Y, spp. 3), *Rostellularia* Rehb. (Y, spp. 3), *Rungia* Nees (Y, spp. 6; T, spp. 2), *Semnostachya* Bremek. (Y, spp. 2), *Sericocalyx* Bremek. (Y, sp. 1), *Staurogyne* Wall. (Y, spp. 6; T, spp. 2), *Strobilanthes* Blume (Y, spp. 10; T, spp. 6), *Sympagis* (Nees) Bremek. (Y, sp. 1), *Tarphochlamys* Bremek. (Y, sp. 1), *Tetraglochidium* Bremek. (Y, spp. 2), *Tetragoga* Bremek. (Y, sp. 1), *Thunbergia* Retz. (Y, spp. 6).
- Acoraceae** (Y, gen. 1; T, gen. 1): *Acorus* L. (Y, spp. 4; T, sp. 1).
- Actinidiaceae** (Y, gen. 3; T, gen. 1): *Actinidia* Lindl. (Y, spp. 23; T, spp. 6), *Clematoclethra* (Franch.) Maxim. (Y, spp. 2), *Saurauia* Willd. (Y, spp. 12).
- Adoxaceae** (Y, gen. 2; T, gen. 1): *Adoxa* L. (Y, sp. 1), *Viburnum* L. (Y, spp. 43; T, spp. 14).
- Akaniaceae** (Y, gen. 1; T, gen. 1): *Bretschneidera* Hemsl. (Y, sp. 1; T, sp. 1).
- Alismataceae** (Y, gen. 3; T, gen. 3): *Alisma* L. (Y, sp. 1; T, sp. 1), *Caldesia* Parl. (Y, sp. 1; T, sp. 1), *Sagittaria* L. (Y, spp. 4; T, spp. 2).
- Amaranthaceae** (Y, gen. 9; T, gen. 8): *Achyranthes* L. (Y, spp. 2; T, spp. 2), *Aerva* Forssk. (Y, spp. 2; T, sp. 1), *Alternanthera* Forssk. (Y, spp. 4; T, spp. 4), *Amaranthus* L. (Y, spp. 7; T, spp. 4), *Celosia* L. (Y, spp. 2; T, spp. 2), *Cyathula* Blume (Y, spp. 3; T, sp. 1), *Deeringia* R. Br. (Y,

sp. 1; T, spp. 2), *Philoxerus* R. Br. (T, sp. 1), *Psilotrichum* Blume (Y, sp. 1), *Stilbanthus* Hook. f. (Y, sp. 1)

Amaryllidaceae (Y, gen. 5; T, gen. 3): *Allium* L. (Y, spp. 25; T, spp. 2), *Crinum* L. (Y, spp. 2; T, sp. 1), *Lycoris* Herb. (Y, spp. 4; T, sp. 1), *Narcissus* L. (Y, sp. 1), *Nothoscordum* Kunth (Y, sp. 1).

Anacardiaceae (Y, gen. 15; T, gen. 4): *Buchanania* Spreng. (Y, spp. 2; T, sp. 1), *Choerospondias* Burtt & A. W. Hill (Y, sp. 1), *Cotinus* Mill. (Y, spp. 2), *Dobinea* Buch.-Ham. (Y, spp. 2), *Dracontomelon* Blume (Y, spp. 2), *Drimycarpus* Hook. f. (Y, spp. 2), *Lannea* A. Rich. (Y, sp. 1), *Mangifera* L. (Y, spp. 5), *Pegia* Colebr. (Y, spp. 2), *Pistacia* L. (Y, spp. 2; T, sp. 1), *Rhus* L. (Y, spp. 5; T, spp. 4), *Semecarpus* L. f. (Y, spp. 2; T, spp. 2), *Spondias* L. (Y, spp. 3), *Terminthia* Bernh. (Y, sp. 1), *Toxicodendron* Mill. (Y, spp. 13).

Annonaceae (Y, gen. 15; T, gen. 3): *Alphonsea* Hook. f. & Thomson (Y, spp. 5), *Artabotrys* R. Br. (Y, spp. 5), *Cyathostemma* Griff. (Y, sp. 1), *Dasymaschalon* (Hook. f. & Thomson) Dalle Torre & Harms (Y, spp. 2), *Desmos* Lour. (Y, spp. 4), *Fissistigma* Griff. (Y, spp. 16; T, spp. 2), *Goniothalamus* (Bl.) Hook. f. & Thomson (Y, spp. 5; T, sp. 1), *Mezzettiopsis* Ridl. (Y, sp. 1), *Miliusa* Lesch. (Y, spp. 4), *Mitrephora* (Bl.) Hook. f. & Thomson (Y, spp. 3), *Orophea* Blume (Y, spp. 2), *Phaeanthus* Hook. f. & Thomson (Y, sp. 1), *Polyalthia* Blume (Y, spp. 10; T, sp. 1), *Pseuduvaria* Miq. (Y, sp. 1), *Uvaria* L. (Y, spp. 5).

Apocynaceae (Y, gen. 48; T, gen. 19): *Aganosma* G. Don (Y, spp. 4), *Alstonia* R. Br. (Y, spp. 4), *Alyxia* Banks (Y, spp. 9; T, spp. 2), *Amalocalyx* Pierre (Y, sp. 1), *Anodendron* A. DC. (Y, sp. 1; T, spp. 2), *Asclepias* L. (Y, sp. 1; T, sp. 1), *Beaumontia* Wall. (Y, spp. 4), *Belostemma* Wall. (Y, spp. 2), *Biondia* Schl. (Y, spp. 2), *Bousigonia* Pierre (Y, spp. 2), *Brachystelma* R. Br. (Y, sp. 1), *Calotropis* R. Br. (Y, spp. 2), *Carissa* L. (Y, spp. 2), *Cerbera* L. (T, sp. 1), *Ceropegia* L. (Y, spp. 8), *Chonemorpha* G. Don (Y, spp. 6), *Cynanchum* L. (Y, spp. 23; T, spp. 4), *Dischidia* R. Br. (Y, spp. 4; T, sp. 1), *Dolichopetalum* Tsiang (Y, sp. 1), *Dregea* E. Mey. (Y, spp. 3; T, sp. 1), *Epigynum* Wight (Y, sp. 1), *Ervatamia* (A. DC.) Stapf (Y, spp. 8), *Gongronema* (Endl.) Decne. (Y, sp. 1), *Gymnema* R. Br. (Y, spp. 7; T, sp. 1), *Heterostemma* Wight & Arn. (Y, spp. 6; T, sp. 1), *Holarrhena* R. Br. (Y, sp. 1; T, sp. 1), *Holostemma* R. Br. (Y, sp. 1), *Hoya* R. Br. (Y, spp. 15; T, sp. 1), *Ichnocarpus* R. Br. (Y, sp. 1), *Kopsia* Blume (Y, sp. 1), *Marsdenia* R. Br. (Y, spp. 15; T, spp. 2), *Melodinus* J. R. Forst. & G. Forst. (Y, spp. 6; T, sp. 1), *Metaplexis* R. Br. (Y, sp. 1), *Parameria* Benth. (Y, sp. 1), *Paravallaris* Pierre ex Hua (Y, spp. 2), *Parepigynum* Tsiang & P. T. Li (Y, sp. 1), *Parsonsia* R. Br. (T, sp. 1), *Pentasacme* Wall. (Y, sp. 1), *Pottsia* Hook. & Arn. (Y, spp. 3), *Raphistemma* Wall. (Y, sp. 1), *Rauwolfia* L. (Y, spp. 6; T, sp. 1), *Sindechites* Oliv. (Y, sp. 1), *Stephanotis* Thouars (Y, spp. 2), *Strophanthus* DC. (Y, spp. 4), *Tabernaemontana* L. (T, spp. 2), *Telosma* Coville (Y, spp. 2; T, sp. 1), *Thevetia* L. (Y, sp. 1), *Trachelospermum* Lem. (Y, spp. 7; T, spp. 4), *Tylophora* R. Br. (Y, spp. 10; T, spp. 3), *Vallaris* Burm. f. (Y, sp. 1), *Wrightia* R. Br. (Y, spp. 5).

Aponogetonaceae (T, gen. 1): *Aponogeton* L. f. (Y, sp. 1; T, sp. 1).

Aquifoliaceae (Y, gen. 1; T, gen. 1): *Ilex* L. (Y, spp. 79; T, spp. 21).

Araceae (Y, gen. 21; T, gen. 14): *Aglaonema* Schott (Y, spp. 2), *Alocasia* Schott (Y, spp. 3; T, spp. 2), *Amorphophallus* Blume (Y, spp. 8; T, spp. 4), *Anadendrum* Schott (Y, spp. 2), *Arisaema* Mart. (Y, spp. 39; T, spp. 9), *Colocasia* Schott (Y, spp. 5; T, spp. 4), *Cryptocoryne* Fisch. (Y, sp. 1), *Epipremnopsis* Engl. (Y, spp. 2), *Epipremnum* Schott (Y, sp.

1; T, spp. 2), *Gonatanthus* Klotzsch (Y, spp. 2), *Hapaline* Schott (Y, sp. 1), *Homalomena* Schott (Y, spp. 2; T, spp. 2), *Lasia* Lour. (Y, sp. 1), *Pinellia* Ten. (Y, spp. 2; T, sp. 1), *Pistia* L. (Y, sp. 1; T, sp. 1), *Pothoidium* Schott (T, sp. 1), *Pothos* L. (Y, spp. 5; T, sp. 1), *Remusatia* Schott (Y, spp. 2; T, sp. 1), *Rhaphidophora* Hassk. (Y, spp. 9; T, spp. 2), *Sauromatum* Schott (Y, sp. 1), *Schismatoglottis* Zoll. & Moritzi (T, sp. 1), *Steudnera* K. Koch (Y, spp. 2), *Typhonium* Schott (Y, spp. 8; T, spp. 2).

Araliaceae (Y, gen. 18; T, gen. 9): *Acanthopanax* Miq. (Y, spp. 9), *Aralia* L. (Y, spp. 18; T, spp. 4), *Brassaiopsis* Decne. & Planch. (Y, spp. 20), *Dendropanax* Decne. & Planch. (Y, spp. 7; T, spp. 2), *Diplopanax* Hand.-Mazz. (Y, sp. 1), *Eleutherococcus* Maxim. (T, sp. 1), *Fatsia* Decne. & Planch. (Y, spp. 2; T, sp. 1), *Hedera* L. (Y, sp. 1), *Heteropanax* Seem. (Y, spp. 4), *Kalopanax* Miq. (Y, sp. 1), *Macropanax* Miq. (Y, spp. 5), *Merrillipanax* H. L. Li (Y, spp. 2), *Metapanax* J. Wen & Frodin (Y, spp. 2), *Osmoxylon* Miq. (T, sp. 1), *Panax* L. (Y, spp. 4), *Pentapanax* Seem. (Y, spp. 8; T, sp. 1), *Schefflera* J. R. Forst. & G. Forst. (Y, spp. 30; T, spp. 4), *Sinopanax* H. L. Li (T, sp. 1), *Tetrapanax* K. Koch (Y, sp. 1; T, sp. 1), *Trevesia* Vis. (Y, sp. 1), *Tupidanthus* Hook. f. & Thomson (Y, sp. 1).

Aristolochiaceae (Y, gen. 2; T, gen. 2): *Aristolochia* L. (Y, spp. 24; T, spp. 5), *Asarum* L. (Y, spp. 7; T, spp. 6).

Asclepiadaceae (Y, gen. 10; T, gen. 2): *Adelostemma* Hook. f. (Y, sp. 1), *Cryptolepis* R. Br. (Y, spp. 2; T, sp. 1), *Genianthus* Hook. f. (Y, sp. 1), *Goniostemma* Wight (Y, sp. 1), *Jasminanthes* Blume (Y, sp. 1; T, sp. 1), *Myriopterion* Griff. (Y, sp. 1), *Oxystelma* R. Br. (Y, sp. 1), *Periploca* L. (Y, spp. 3), *Secamone* R. Br. (Y, spp. 4), *Streptocaulon* Wight & Arn. (Y, spp. 2), *Toxocarpus* Wight & Arn. (Y, spp. 5).

Asparagaceae (Y, gen. 3; T, gen. 3): *Agave* L. (Y, spp. 3; T, sp. 1), *Asparagus* L. (Y, spp. 13; T, sp. 1), *Dracaena* Vand. ex L. (Y, spp. 6; T, spp. 2).

Asteraceae (Y, gen. 132; T, gen. 76): *Acanthospermum* Schrank (Y, sp. 1), *Achillea* L. (Y, sp. 1), *Acmella* Rich. (T, spp. 2), *Adenocaulon* Hook. (Y, sp. 1), *Adenostemma* J. R. Forst. & G. Forst. (Y, sp. 1; T, sp. 1), *Ageratina* Spach (Y, sp. 1; T, sp. 1), *Ageratum* L. (Y, spp. 2; T, spp. 2), *Ainsliaea* DC. (Y, spp. 27; T, spp. 3), *Ajania* Poljakov (Y, spp. 7), *Ambrosia* L. (T, sp. 1), *Anaphalis* DC. (Y, spp. 26; T, spp. 4), *Anisopappus* Hook. & Arn. (Y, sp. 1), *Arctium* L. (Y, sp. 1), *Artemisia* L. (Y, spp. 54; T, spp. 15), *Aster* L. (Y, spp. 36; T, spp. 16), *Atractylodes* DC. (Y, spp. 2), *Bidens* L. (Y, spp. 5; T, spp. 4), *Blainvillea* Cass. (Y, sp. 1), *Blumea* DC. (Y, spp. 26; T, spp. 11), *Blumeopsis* Gagnep. (Y, sp. 1), *Calendula* L. (Y, sp. 1), *Callistephus* Cass. (Y, sp. 1), *Camchaya* Gagnep. (Y, sp. 1), *Carduus* L. (Y, spp. 2), *Carpesium* L. (Y, spp. 11; T, spp. 5), *Carthamus* L. (Y, sp. 1), *Centaurea* L. (Y, sp. 1), *Centipeda* Lour. (Y, sp. 1; T, sp. 1), *Cephalorrhynchus* Boiss. (Y, sp. 1), *Chaetoseris* C. Shih (Y, spp. 14), *Chrysanthemum* L. (Y, spp. 2), *Cicerbita* Wallr. (Y, sp. 1), *Cichorium* L. (T, sp. 1), *Cirsium* Mill. (Y, spp. 16; T, spp. 8), *Cissampelopsis* (DC.) Miq. (Y, spp. 5), *Conyza* Less. (Y, spp. 8; T, spp. 6), *Coreopsis* L. (Y, spp. 2), *Cotula* L. (Y, sp. 1; T, sp. 1), *Crassocephalum* Moench (Y, sp. 1; T, sp. 1), *Cremanthodium* Benth. (Y, spp. 36), *Crepidiastrum* Nakai (T, spp. 2), *Crepis* L. (Y, spp. 7), *Crossostephium* Less. (T, sp. 1), *Cyathocline* Cass. (Y, sp. 1), *Dendranthema* (DC.) Des Moul. (Y, spp. 4; T, spp. 4), *Dichrocephala* L'Hér. ex DC. (Y, spp. 3; T, sp. 1), *Diplazoptilon* Y. Ling (Y, sp. 1), *Doellingeria* Nees (Y, sp. 1), *Dolomiaea* DC. (Y, spp. 6), *Doronicum* L. (Y, spp. 2), *Dubyaea* DC. (Y, spp. 5), *Echinops* L. (T, sp. 1), *Eclipta*

- L. (Y, sp. 1; T, spp. 2), *Elephantopus* L. (Y, sp. 1; T, spp. 2), *Emilia* Cass. (Y, spp. 2; T, sp. 1), *Enydra* Lour. (Y, sp. 1), *Epaltes* Cass. (Y, sp. 1; T, sp. 1), *Erechtites* Raf. (Y, sp. 1; T, spp. 2), *Erigeron* L. (Y, spp. 8; T, spp. 2), *Ethulia* L. f. (Y, sp. 1), *Eupatorium* L. (Y, spp. 6; T, spp. 7), *Faberia* Hemsl. (Y, spp. 3), *Farfugium* Lindl. (T, sp. 1), *Formania* W. W. Sm. & Small (Y, sp. 1), *Galinsoga* Ruiz & Pav. (Y, sp. 1; T, spp. 2), *Gerbera* L. (Y, spp. 5; T, sp. 1), *Glossocardia* Cass. (T, sp. 1), *Gnaphalium* L. (Y, spp. 7; T, spp. 8), *Gochnatia* Kunth (Y, sp. 1), *Grangea* Adans. (Y, sp. 1; T, sp. 1), *Gynura* Cass. (Y, spp. 8; T, spp. 3), *Hemisteptia* Bunge (Y, sp. 1; T, sp. 1), *Heteropappus* Less. (Y, sp. 1), *Hieracium* L. (Y, sp. 1; T, sp. 1), *Hippolytia* Poljakov (Y, spp. 2), *Hypochaeris* L. (T, sp. 1), *Inula* L. (Y, spp. 9), *Ixeridium* (A. Gray) Tzvel. (Y, spp. 4; T, spp. 2), *Ixeris* Cass. (Y, sp. 1; T, spp. 6), *Kalimeris* Cass. (Y, sp. 1), *Lactuca* L. (Y, spp. 2), *Lagenophora* Cass. (Y, sp. 1; T, sp. 1), *Laggera* Sch.-Bip. (Y, spp. 2; T, sp. 1), *Lapsana* L. (Y, sp. 1), *Lapsanastrum* Pak & K. Bremer (T, spp. 2), *Launaea* Cass. (Y, sp. 1), *Leibnitzia* Cass. (Y, spp. 4), *Leontopodium* R. Brown (Y, spp. 14; T, sp. 1), *Ligularia* Cass. (Y, spp. 57; T, spp. 3), *Microglossa* DC. (Y, sp. 1; T, sp. 1), *Mikania* Willd. (Y, sp. 1; T, sp. 1), *Mulgedium* Cass. (Y, spp. 3), *Myriactis* Less. (Y, spp. 4; T, sp. 1), *Nannoglottis* Maxim. (Y, spp. 3), *Nemosencio* (Kitam.) B. Nord. (Y, spp. 3; T, sp. 1), *Neopallasia* (Pall.) Poljak. (Y, sp. 1), *Notoseris* C. Shih (Y, spp. 3; T, sp. 1), *Nouelia* Franch. (Y, sp. 1), *Paraixeris* Nakai (Y, spp. 2), *Paramicrorhynchus* Kirp. (Y, sp. 1), *Paraprenanthes* C. C. Chang (Y, spp. 6; T, sp. 1), *Parasenecio* W. W. Sm. & Small (Y, spp. 15; T, spp. 3), *Parthenium* L. (Y, spp. 2), *Pentanema* Cass. (Y, sp. 1), *Pertya* Sch.-Bip. (Y, spp. 3; T, sp. 1), *Petasites* Mill. (Y, spp. 2; T, sp. 1), *Picris* L. (Y, spp. 3), *Piloselloides* (Less.) C. Jeffr. (Y, sp. 1), *Pluchea* Cass. (Y, sp. 1; T, spp. 4), *Prenanthes* L. (Y, spp. 4), *Pseudelephantopus* Rohr (T, sp. 1), *Pterocypsella* C. Shih (Y, spp. 3; T, spp. 3), *Pyrethrum* Zinn. (Y, spp. 2), *Rhynchospermum* Reinw. (Y, sp. 1; T, sp. 1), *Saussurea* DC. (Y, spp. 90; T, spp. 5), *Senecio* L. (Y, spp. 28; T, spp. 7), *Serratula* L. (Y, sp. 1), *Sheareria* S. Moore (Y, sp. 1), *Sigesbeckia* L. (Y, spp. 3; T, sp. 1), *Sinacalia* H. Rob. & Brettell (Y, sp. 1), *Sinosenecio* B. Nord. (Y, spp. 7), *Solidago* L. (Y, sp. 1; T, sp. 1), *Soliva* Ruiz & Pav. (T, spp. 2), *Sonchus* L. (Y, spp. 6; T, spp. 3), *Soroseris* Stebb. (Y, spp. 3), *Sphaeranthus* L. (Y, spp. 3; T, sp. 1), *Spilanthes* Jacq. (Y, spp. 2), *Stebbinsia* Lipsch. (Y, sp. 1), *Stenoseric* C. Shih (Y, spp. 4), *Syncalathium* Lipsch. (Y, sp. 1), *Synedrella* Gaertn. (Y, sp. 1; T, sp. 1), *Syneilesis* Maxim. (T, spp. 2), *Synotis* (C. B. Clarke) C. Jeffrey & Y. L. Che (Y, spp. 27), *Taraxacum* F. H. Wigg (Y, spp. 12; T, spp. 2), *Tephrosieris* (Reichenb.) Reichenb. (Y, sp. 1; T, spp. 2), *Thespis* DC. (Y, sp. 1), *Tragopogon* L. (Y, sp. 1), *Tricholepis* DC. (Y, sp. 1), *Tridax* L. (Y, sp. 1; T, sp. 1), *Tussilago* L. (Y, sp. 1), *Vernonia* Schreb. (Y, spp. 22; T, spp. 5), *Wedelia* Jacq. (Y, spp. 3; Y, T, spp. 4), *Xanthium* L. (Y, sp. 1; T, sp. 1), *Xanthopappus* C. Winkl. (Y, sp. 1), *Youngia* Cass. (Y, spp. 14; T, sp. 1).
- Balanophoraceae** (Y, gen. 2; T, gen. 1): *Balanophora* J. R. Forst. & G. Forst. (Y, spp. 6; T, spp. 5), *Rhopalocnemis* Jungh. (Y, sp. 1).
- Balsaminaceae** (Y, gen. 1; T, gen. 1): *Impatiens* L. (Y, spp. 112; T, spp. 3).
- Begoniaceae** (Y, gen. 1; T, gen. 1): *Begonia* L. (Y, spp. 92; T, spp. 13).
- Berberidaceae** (Y, gen. 8; T, gen. 3): *Berberis* L. (Y, spp. 88; T, spp. 7), *Caulophyllum* Michx. (Y, sp. 1), *Diphylleia* Michx. (Y, sp. 1), *Dysosma* Woodson (Y, spp. 5; T, sp. 1), *Epimedium* L. (Y, spp. 2), *Mahonia* Nutt. (Y, spp. 17; T, spp. 2), *Nandina* Thunb. (Y, sp. 1), *Sinopodophyllum* T. S. Ying (Y, sp. 1).
- Betulaceae** (Y, gen. 6; T, gen. 3): *Alnus* Mill. (Y, spp. 3; T, sp. 1), *Betula* L. (Y, spp. 11), *Carpinus* L. (Y, spp. 14; T, spp. 3), *Corylus* L. (Y, spp. 6; T, sp. 1), *Ostrya* Scop. (Y, sp. 1), *Ostryopsis* Decne. (Y, sp. 1).
- Bignoniaceae** (Y, gen. 12; T, gen. 2): *Campsis* Lour. (Y, sp. 1), *Catalpa* Scop. (Y, spp. 3), *Dolichandrone* (Fenzl) Seem. (Y, spp. 2), *Incarvillea* Juss. (Y, spp. 6), *Mayodendron* Kurz (Y, sp. 1), *Millingtonia* L. f. (Y, sp. 1), *Nyctocalos* Teijsm. & Binn. (Y, spp. 2), *Oroxylum* Vent. (Y, sp. 1), *Pauletopia* Steenis (Y, sp. 1), *Paulownia* Sieb. & Zucc. (Y, spp. 4; T, spp. 3), *Radermachera* Zoll. & Moritz (Y, spp. 4; T, sp. 1), *Stereospermum* Cham. (Y, spp. 3).
- Bombacaceae** (Y, gen. 1; T, gen. 1): *Bombax* L. (Y, spp. 2; T, sp. 1).
- Boraginaceae** (Y, gen. 20; T, gen. 13): *Antiotrema* Hand.-Mazz. (Y, sp. 1), *Bothriospermum* Bunge (Y, spp. 2; T, sp. 1), *Carmona* Cav. (T, sp. 1), *Chionocharis* I. M. Johnst. (Y, sp. 1), *Coldenia* L. (T, sp. 1), *Cordia* L. (Y, spp. 2; T, sp. 1), *Cynoglossum* L. (Y, spp. 4; T, spp. 3), *Ehretia* P. Browne (Y, spp. 7; T, spp. 5), *Eritrichium* Schrad. (Y, spp. 3), *Heliotropium* L. (Y, spp. 3; T, spp. 2), *Lasiocaryum* I. M. Johnst. (Y, spp. 2), *Lithospermum* L. (Y, spp. 2; T, sp. 1), *Microcaryum* I. M. Johnst. (Y, sp. 1), *Microula* Benth. (Y, spp. 8), *Myosotis* L. (Y, spp. 2; T, sp. 1), *Onosma* L. (Y, spp. 14), *Rotula* Lour. (Y, sp. 1), *Sinojohnstonia* Hu (Y, sp. 1), *Thyrocarpus* Hance (Y, sp. 1; T, sp. 1), *Tournefortia* L. (Y, sp. 1; T, spp. 2), *Trichodesma* R. Br. (Y, sp. 1; T, sp. 1), *Trigonotis* Steven (Y, spp. 14; T, spp. 3).
- Borthwickiaceae** (Y, gen. 1): *Borthwickia* W. W. Sm. (Y, sp. 1).
- Burmanniaceae** (Y, gen. 1; T, gen. 3): *Burmannia* L. (Y, spp. 7; T, spp. 3), *Gymnosiphon* Blume (T, sp. 1), *Thismia* Griff. (T, sp. 1).
- Burseraceae** (Y, gen. 3): *Canarium* L. (Y, spp. 7), *Garuga* Roxb. (Y, spp. 4), *Protium* Burm. f. (Y, spp. 2).
- Butomaceae** (Y, gen. 2): *Limnocharis* Bonpl. (Y, sp. 1), *Tenagocharis* Hochst. (Y, sp. 1).
- Buxaceae** (Y, gen. 3; T, gen. 3): *Buxus* L. (Y, spp. 8; T, sp. 1), *Pachysandra* Michx. (Y, spp. 2; T, sp. 1), *Sarcococca* Lindl. (Y, spp. 6; T, sp. 1).
- Cabombaceae** (Y, gen. 1; T, gen. 1): *Brasenia* Schreb. (Y, sp. 1; T, sp. 1).
- Calycanthaceae** (Y, gen. 1): *Chimonanthus* Lindl. (Y, spp. 2).
- Campanulaceae** (Y, gen. 13; T, gen. 9): *Adenophora* Fisch. (Y, spp. 7; T, spp. 2), *Asyneuma* Griseb. & Schenk (Y, sp. 1), *Campanula* L. (Y, spp. 12; T, sp. 1), *Campanumoea* Blume (Y, spp. 4), *Codonopsis* Wall. (Y, spp. 19; T, sp. 1), *Cyananthus* Wall. ex Benth. (Y, spp. 19), *Cyclocodon* Griff. (T, sp. 1), *Hippobroma* G. Don (T, sp. 1), *Homocodon* D. Y. Hong (Y, sp. 1), *Leptocodon* (Hook. f.) Lem. (Y, spp. 2), *Lobelia* L. (Y, spp. 15; T, spp. 4), *Peracarpa* Hook. f. & Thomson (Y, sp. 1; T, sp. 1), *Platycodon* A. DC. (Y, sp. 1), *Pratia* Gaudich. (Y, spp. 2), *Triodanis* Raf. Greene (T, sp. 1), *Wahlenbergia* Schrad. (Y, sp. 1; T, sp. 1).
- Cardiopteridaceae** (Y, gen. 1): *Cardiopteris* Wall. (Y, sp. 1).
- Capparidaceae** (Y, gen. 4; T, gen. 2): *Capparis* L. (Y, spp. 19; T, spp. 4), *Cleome* L. (Y, spp. 6; T, spp. 3), *Crateva* L. (Y, spp. 3), *Stixis* Lour. (Y, sp. 1).
- Caprifoliaceae** (Y, gen. 18; T, gen. 7): *Abelia* R. Br. (Y, spp. 6; T, sp. 1), *Acanthocalyx* (DC.) M. Cannon (Y, spp. 3), *Cephalostigma* A. DC. (Y, sp. 1), *Cryptothladia* (Bunge) M. Cannon (Y, sp. 1), *Dipelta* Maxim. (Y, sp. 1), *Dipsacus* L. (Y, spp. 5), *Leycesteria* Wall. (Y, spp. 4), *Lonicera* L. (Y, spp. 39; T, spp. 7), *Nardostachys* DC. (Y, sp. 1), *Patrinia* Juss. (Y, spp. 4; T, spp. 4), *Pterocephalus* Adans. (Y, spp. 2), *Sambucus* L. (Y, spp. 3; T, sp. 1), *Scabiosa* L. (Y, sp. 1;

T, sp. 1), *Symphoricarpos* Duhamel (Y, sp. 1), *Triosteum* L. (Y, sp. 1), *Triplostegia* Wall. (Y, spp. 2; T, sp. 1), *Valeriana* L. (Y, spp. 8; T, spp. 3), *Weigela* Thunb. (Y, sp. 1).

Carlemanniaceae (Y, gen. 2): *Carlemannia* Benth. (Y, sp. 1), *Silvianthus* Hook. f. (Y, sp. 1).

Caryophyllaceae (Y, gen. 17; T, gen. 11): *Arenaria* L. (Y, spp. 43; T, spp. 3), *Brachystemma* D. Don (Y, sp. 1), *Cerastium* L. (Y, spp. 6; T, spp. 2), *Cucubalus* L. (Y, sp. 1; T, sp. 1), *Dianthus* L. (Y, spp. 5; T, spp. 3), *Drymaria* Willd. (Y, sp. 1; T, sp. 1), *Lychnis* L. (Y, spp. 3), *Moehringia* L. (T, sp. 1), *Myosoton* Moench (Y, sp. 1), *Polycarpaea* Lam. (Y, sp. 1; T, sp. 1), *Polycarpon* L. (Y, sp. 1), *Psammosilene* W. C. Wu & C. Y. Wu (Y, sp. 1), *Pseudostellaria* Pax (Y, spp. 3), *Sagina* L. (Y, spp. 2; T, spp. 2), *Silene* L. (Y, spp. 49; T, spp. 5), *Spergula* L. (T, sp. 1), *Spergularia* (Pers.) J. & C. Presl (Y, sp. 1), *Stellaria* L. (Y, spp. 19; T, spp. 5), *Vaccaria* Wolf (Y, sp. 1).

Celastraceae (Y, gen. 10; T, gen. 6): *Celastrus* L. (Y, spp. 18; T, spp. 4), *Euonymus* L. (Y, spp. 56; T, spp. 10), *Glyptopetalum* Thwaites (Y, spp. 5), *Loeseneriella* A. C. Sm. (Y, spp. 3), *Maytenus* Molina (Y, spp. 15; T, spp. 2), *Microtropis* Wall. (Y, spp. 18; T, spp. 2), *Perrottetia* Kunth (Y, sp. 1; T, sp. 1), *Pristimera* Miers (Y, spp. 3), *Salacia* L. (Y, spp. 6), *Tripterygium* Hook. f. (Y, sp. 1; T, sp. 1).

Cephalotaxaceae (Y, gen. 1; T, gen. 1): *Cephalotaxus* Sieb. & Zucc. (Y, spp. 6; T, sp. 1).

Ceratophyllaceae (Y, gen. 1; T, gen. 1): *Ceratophyllum* L. (Y, spp. 2; T, spp. 3).

Cercidiphyllaceae (Y, gen. 1): *Cercidiphyllum* Sieb. & Zucc. (Y, sp. 1).

Chenopodiaceae (Y, gen. 5; T, gen. 3): *Acroglochin* Schrad. (Y, spp. 2), *Atriplex* L. (T, spp. 2), *Axyris* L. (Y, sp. 1), *Chenopodium* L. (Y, spp. 6; T, spp. 5), *Kochia* Roth (Y, sp. 1), *Salsola* L. (Y, sp. 1), *Suaeda* Forssk. (T, sp. 1).

Chloranthaceae (Y, gen. 2; T, gen. 2): *Chloranthus* Sw. (Y, spp. 4; T, sp. 1), *Sarcandra* Gardn. (Y, spp. 2; T, sp. 1).

Circaeasteraceae (Y, gen. 1): *Circaeaster* Maxim. (Y, sp. 1).

Clethraceae (Y, gen. 1): *Clethra* L. (Y, spp. 5).

Clusiaceae (Y, gen. 4; T, gen. 2): *Calophyllum* L. (Y, spp. 2; T, spp. 2), *Garcinia* L. (Y, spp. 13; T, spp. 3), *Mesua* L. (Y, sp. 1), *Ochrocarpos* Noronha (Y, sp. 1).

Combretaceae (Y, gen. 4; T, gen. 2): *Anogeissus* Wall. (Y, sp. 1), *Combretum* Loebl. (Y, spp. 10), *Lumnitzera* Willd. (T, sp. 1), *Quisqualis* L. (Y, spp. 2), *Terminalia* L. (Y, spp. 6; T, sp. 1).

Commelinaceae (Y, gen. 11; T, gen. 8): *Amischotolype* Hassk. (Y, spp. 2; T, sp. 1), *Belosynapsis* Hassk. (Y, sp. 1; T, spp. 2), *Commelina* L. (Y, spp. 6; T, spp. 5), *Cyanotis* D. Don (Y, spp. 3; T, spp. 2), *Dictyospermum* Wight (Y, spp. 2), *Floscopa* Lour. (Y, spp. 2; T, sp. 1), *Murdannia* Royle (Y, spp. 14; T, spp. 4), *Polliia* Thunb. (Y, spp. 5; T, spp. 3), *Porandra* D. Y. Hong (Y, spp. 2), *Rhopalephora* Hassk. (T, sp. 1), *Spatholirion* Ridl. (Y, spp. 2), *Streptolirion* Edgew. (Y, spp. 2).

Connaraceae (Y, gen. 3; T, gen. 2): *Connarus* L. (Y, sp. 1; T, sp. 1), *Rourea* Aubl. (Y, sp. 1; T, sp. 1), *Roureopsis* Planch. (Y, sp. 1).

Convolvulaceae (Y, gen. 16; T, gen. 14): *Argyreia* Lour. (Y, spp. 16; T, sp. 1), *Blinkworthia* Choisy (Y, sp. 1), *Calonyction* Choisy (Y, spp. 3), *Calystegia* R. Br. (Y, spp. 2; T, sp. 1), *Convolvulus* L. (Y, sp. 1), *Cuscuta* L. (Y, spp. 5; T, spp. 4), *Dichondra* J. R. Forst. & G. Forst. (Y, sp. 1; T, sp. 1), *Erycibe* Roxb. (Y, spp. 4; T, sp. 1), *Evolvulus* L. (Y, sp. 1; T, sp. 1), *Hewittia* Wight & Arn. (Y, sp. 1; T, sp. 1), *Ipomoea* L. (Y, spp. 12; T, spp. 21), *Jacquemontia* Choisy (Y, sp. 1; T, spp. 2), *Lepistemon* Blume (T, sp. 1), *Merremia* Dennst. (Y, spp. 12; T, spp. 7), *Neuropeltis* Wall.

(Y, sp. 1), *Operculina* Silva Manso (Y, sp. 1; T, sp. 1), *Porana* Burm. f. (Y, spp. 12), *Stictocardia* Hallier f. (T, sp. 1), *Xenostegia* D. F. Austin & G. W. Staples (T, sp. 1).

Coriariaceae (Y, gen. 1; T, gen. 1): *Coriaria* L. (Y, spp. 2; T, sp. 1).

Cornaceae (Y, gen. 8; T, gen. 5): *Alangium* Lam. (Y, spp. 7; T, sp. 1), *Aucuba* Thunb. (Y, spp. 16; T, spp. 2), *Cornus* L. (= *Swida* Opiz) (Y, spp. 13; T, spp. 2), *Davidia* Baill. (Y, sp. 1), *Dendrobenthamia* Hutch. (Y, spp. 9; T, sp. 1), *Helwingia* Willd. (Y, spp. 4; T, sp. 1), *Macrocarpium* (Spach.) Nakai (Y, sp. 1), *Mastixia* Blume (Y, spp. 2).

Crassulaceae (Y, gen. 7; T, gen. 4): *Bryophyllum* Salisb. (Y, sp. 1; T, sp. 1), *Hylotelephium* H. Ohba (Y, spp. 2; T, sp. 1), *Kalanchoe* Adans. (Y, spp. 2; T, spp. 3), *Rhodiola* L. (Y, spp. 23), *Sedum* L. (Y, spp. 39; T, spp. 14), *Sinocrassula* A. Berger (Y, spp. 5), *Tillaea* L. (Y, spp. 2).

Cruciferae (Y, gen. 31; T, gen. 14): *Aphragmus* Andr. ex DC. (Y, sp. 1), *Arabidopsis* Heynh. (Y, spp. 4), *Arabis* L. (Y, spp. 2; T, spp. 3), *Barbarea* W. T. Aiton (T, spp. 2), *Brassica* L. (Y, spp. 11), *Braya* Sternb. & Hoppe (Y, spp. 2), *Capsella* Medik. (Y, sp. 1; T, sp. 1), *Cardamine* L. (Y, spp. 20; T, spp. 5), *Cheiranthus* L. (Y, spp. 2), *Cochlearia* L. (T, sp. 1), *Coronopus* Zinn (Y, sp. 1; T, spp. 2), *Descurainia* Webb & Berthel. (Y, sp. 1), *Dimorphostemon* Kitag. (Y, spp. 2), *Dipoma* Franch. (Y, sp. 1), *Draba* L. (Y, spp. 20; T, sp. 1), *Erysimum* L. (Y, spp. 6), *Eutrema* R. Br. (Y, spp. 4; T, sp. 1), *Hemilophia* Franch. (Y, sp. 1), *Isatis* L. (Y, spp. 2), *Lepidium* L. (Y, spp. 3; T, sp. 1), *Loxostemon* Hook. f. & Thomson (Y, spp. 6), *Matthiola* W. T. Aiton (Y, sp. 1), *Megacarpaea* DC. (Y, sp. 1), *Nasturtium* W. T. Aiton (Y, sp. 1; T, sp. 1), *Neomartinella* Pilg. (Y, sp. 1), *Neslia* Desv. (T, sp. 1), *Pegaeophyton* Hayek & Hand.-Mazz. (Y, sp. 1), *Raphanus* L. (Y, spp. 2; T, sp. 1), *Rorippa* Scop. (Y, spp. 6; T, spp. 6), *Sisymbrium* L. (Y, spp. 2; T, spp. 2), *Solmslaubachia* Muschl. (Y, spp. 5), *Staintoniella* H. Hara (Y, sp. 1), *Thlaspi* L. (Y, spp. 3), *Yinshania* Ma & Y. Z. Zhao (Y, sp. 1).

Crypteroniaceae (Y, gen. 1): *Crypteronia* Blume (Y, sp. 1).

Cucurbitaceae (Y, gen. 25; T, gen. 13): *Actinostemma* Griff. (Y, sp. 1; T, sp. 1), *Benincasa* Savi (Y, sp. 1), *Biswarea* Cogn. (Y, sp. 1), *Bolbostemma* Franquet (Y, sp. 1), *Coccinia* Wight & Arn. (Y, sp. 1; T, sp. 1), *Cucumis* L. (Y, spp. 3), *Diplocyclos* (Endl.) T. Post & Kuntze (T, sp. 1), *Gomphogyne* Griff. (Y, sp. 1), *Gymnopetalum* Arn. (Y, spp. 2; T, sp. 1), *Gynostemma* Blume (Y, spp. 8; T, sp. 1), *Hemsleya* Cogn. (Y, spp. 20), *Herpetospermum* Wall. (Y, sp. 1), *Hodgsonia* Hook. f. & Thomson (Y, sp. 1), *Lagenaria* Ser. (Y, sp. 1), *Luffa* Mill. (Y, spp. 2), *Momordica* L. (Y, spp. 4; T, spp. 2), *Mukia* Arn. (Y, spp. 2; T, sp. 1), *Nealsomitra* Hutch. (Y, sp. 1; T, sp. 1), *Schizopepon* Maxim. (Y, spp. 2), *Sicyos* L. (Y, sp. 1), *Siraitia* Merr. (Y, spp. 2; T, sp. 1), *Solena* Lour. (Y, spp. 2; T, sp. 1), *Thladiantha* Bunge (Y, spp. 9; T, spp. 2), *Trichosanthes* L. (Y, spp. 26; T, spp. 6), *Zanonia* L. (Y, sp. 1), *Zehneria* Endl. (Y, spp. 5; T, spp. 3).

Cupressaceae (Y, gen. 6; T, gen. 3): *Calocedrus* Kurz (Y, sp. 1; T, sp. 1), *Chamaecyparis* Spach. (Y, spp. 3; T, sp. 1), *Cupressus* L. (Y, spp. 3), *Fokienia* A. Henry & H. H. Thomas (Y, sp. 1), *Juniperus* L. (Y, sp. 1; T, spp. 2), *Platycladus* Spach (Y, sp. 1).

Cycadaceae (Y, gen. 1; T, gen. 1): *Cycas* L. (Y, spp. 10; T, sp. 1).

Cyperaceae (Y, gen. 26; T, gen. 25): *Actinoscirpus* (Ohwi) R. W. Haines & Lye (T, sp. 1), *Blysmus* Panz. (Y, sp. 1), *Bolboschoenus* Palla (Y, sp. 1; T, sp. 1), *Bulbostylis* Kunth (Y, spp. 2; T, spp. 2), *Carex* L. (Y, spp. 134; T, spp. 57), *Cladium* P. Browne (Y, sp. 1; T, sp. 1), *Courtoisina* Sojak (Y, sp. 1), *Cyperus* L. (Y, spp. 20; T, spp. 22), *Diplacrum* R.

- Br. (T, sp. 1), *Eleocharis* R. Br. (Y, spp. 10; T, spp. 7), *Eriophorum* L. (Y, sp. 1), *Fimbristylis* Vahl (Y, spp. 23; T, spp. 23), *Fuirena* Rottb. (Y, spp. 3; T, spp. 2), *Gahnia* J. R. (Y, sp. 1; T, sp. 1), *Hypolytrum* Rich. (Y, sp. 1; T, sp. 1), *Isolepis* R. Br. (Y, sp. 1), *Juncellus* (Griseb.) C. B. Clarke (Y, sp. 1), *Kobresia* Willd. (Y, spp. 27), *Kyllinga* Rottb. (Y, spp. 4; T, spp. 2), *Lepironia* Rich. (T, sp. 1), *Lipocarpus* R. Br. (Y, spp. 3; T, spp. 2), *Mariscus* Vahl (Y, spp. 4; T, spp. 5), *Pycnus* P. Beauv. (Y, spp. 6; T, spp. 6), *Remirea* Aubl. (T, sp. 1), *Rhynchospora* Vahl (Y, spp. 3; T, spp. 5), *Schoenoplectus* (Reichb.) Palla (Y, spp. 9; T, spp. 5), *Schoenus* L. (Y, sp. 1; T, spp. 2), *Scirpus* L. (Y, spp. 2; T, sp. 1), *Scleria* P. J. Bergius (Y, spp. 12; T, spp. 8), *Thoracostachyum* Kurz (Y, sp. 1), *Torulinum* Desv. (T, sp. 1), *Trichophorum* Pers. (T, sp. 1).
- Daphniphyllaceae** (Y, gen. 2; T, gen. 1): *Daphniphyllum* Blume (Y, spp. 6; T, spp. 2), *Dichapetalum* Thouars (Y, sp. 1).
- Diapensiaceae** (Y, gen. 3; T, gen. 1): *Berneuxia* Decne. (Y, sp. 1), *Diapensia* L. (Y, spp. 3), *Shortia* Torr. & A. Gray (Y, sp. 1; T, sp. 1).
- Dilleniaceae** (Y, gen. 2): *Dillenia* L. (Y, spp. 3), *Tetracera* L. (Y, sp. 1).
- Dioscoreaceae** (Y, 1 gen.; T, 1 gen.): *Dioscorea* L. (Y, spp. 38; T, spp. 13).
- Dipentodontaceae** (Y, gen. 1): *Dipentodon* Dunn (Y, sp. 1).
- Dipterocarpaceae** (Y, gen. 5): *Dipterocarpus* C. F. Gaertn. (Y, spp. 3), *Hopea* Roxb. (Y, sp. 1), *Parashorea* Kurz (Y, sp. 1), *Shorea* Roxb. (Y, sp. 1), *Vatica* L. (Y, sp. 1).
- Droseraceae** (Y, gen. 1; T, gen. 1): *Drosera* L. (Y, spp. 2; T, spp. 4).
- Ebenaceae** (Y, gen. 1; T, gen. 1): *Diospyros* L. (Y, spp. 22; T, spp. 10).
- Elaeagnaceae** (Y, gen. 2; T, gen. 1): *Elaeagnus* L. (Y, spp. 27; T, spp. 9), *Hippophae* L. (Y, sp. 1).
- Elaeocarpaceae** (Y, gen. 2; T, gen. 2): *Elaeocarpus* L. (Y, spp. 32; T, spp. 4), *Sloanea* L. (Y, spp. 10; T, sp. 1).
- Elatinaceae** (Y, gen. 2; T, gen. 2): *Bergia* L. (Y, sp. 1; T, sp. 1), *Elatine* L. (Y, spp. 2; T, sp. 1).
- Ephedraceae** (Y, gen. 1): *Ephedra* L. (Y, sp. 1).
- Ericaceae** (Y, gen. 19; T, gen. 11): *Agapetes* D. Don ex G. Don (Y, spp. 20), *Arctous* Niedenzu (Y, sp. 1), *Cassiope* D. Don (Y, spp. 9), *Cheilotheca* Hook. f. (Y, spp. 2; T, spp. 2), *Chimaphila* Pursh (Y, sp. 1; T, spp. 2), *Craibiodendron* W. W. Sm. (Y, spp. 4), *Diplarche* Hook. f. & Thomson (Y, spp. 2), *Enkianthus* Lour. (Y, spp. 6; T, sp. 1), *Eremotropa* Andres (Y, spp. 2), *Gaultheria* Kalm ex L. (Y, spp. 18; T, spp. 2), *Leucothoe* D. Don (Y, spp. 2), *Lyonia* Nutt. (Y, spp. 6; T, sp. 1), *Moneses* Salisb. (Y, sp. 1; T, sp. 1), *Monotropa* L. (Y, spp. 2; T, spp. 2), *Orthilia* Raf. (Y, sp. 1), *Pieris* D. Don (Y, sp. 1; T, spp. 2), *Pyrola* L. (Y, spp. 7; T, spp. 3), *Rhododendron* L. (Y, spp. 230; T, spp. 14), *Vaccinium* L. (Y, spp. 45; T, spp. 6).
- Eriocaulaceae** (Y, gen. 1; T, gen. 1): *Eriocaulon* L. (Y, spp. 15; T, spp. 7).
- Erythroxylaceae** (Y, gen. 1): *Erythroxylum* P. Browne (Y, spp. 2).
- Escalloniaceae** (Y, gen. 1): *Polyosma* Blume (Y, sp. 1).
- Eucommiaceae** (Y, gen. 1): *Eucommia* Oliv. (Y, sp. 1).
- Euphorbiaceae** (Y, gen. 48; T, gen. 25): *Acalypha* L. (Y, spp. 7; T, spp. 10), *Actephila* Blume (Y, spp. 2), *Alchornea* Sw. (Y, spp. 6), *Aleurites* J. R. Forst. & G. Forst. (Y, sp. 1), *Andrachne* L. (Y, spp. 6), *Antidesma* L. (Y, spp. 12; T, sp. 1), *Aporosa* Blume (Y, spp. 4), *Baccaurea* Lour. (Y, spp. 2), *Baliospermum* Blume (Y, spp. 3), *Bischofia* Blume (Y, sp. 1; T, sp. 1), *Breynia* J. R. Forst. & G. Forst. (Y, spp. 5; T, sp. 1), *Bridelia* Willd. (Y, spp. 8; T, spp. 2), *Chaetocarpus* Thwaites (Y, sp. 1), *Chamaesyce* Gray (T, spp. 14), *Claoxylon* A. Juss. (Y, spp. 3; T, sp. 1), *Cleidiocarpus* Airy-Shaw (Y, sp. 1), *Cleidion* Blume (Y, spp. 3), *Cleistanthus* Hook. f. (Y, spp. 3), *Cnesmone* Blume (Y, sp. 1), *Croton* L. (Y, spp. 13; T, spp. 2), *Dalechampia* L. (Y, sp. 1), *Deutzianthus* Gagnep. (Y, sp. 1), *Drypetes* Vahl (Y, spp. 8; T, spp. 2), *Endospermum* Benth. (Y, sp. 1), *Epiprinus* Griff. (Y, sp. 1), *Euphorbia* L. (Y, spp. 30; T, spp. 8), *Excoecaria* L. (Y, spp. 2; T, spp. 3), *Flueggea* Willd. (Y, spp. 4; T, spp. 2), *Glochidion* J. R. Forst. & G. Forst. (Y, spp. 15; T, spp. 5), *Homonoia* Lour. (Y, sp. 1; T, sp. 1), *Jatropha* L. (Y, sp. 1), *Lasiococca* Hook. f. (Y, sp. 1), *Liodendron* H. Keng (T, sp. 1), *Macaranga* Thouars (Y, spp. 7; T, spp. 2), *Mallotus* Lour. (Y, spp. 16; T, spp. 5), *Margaritaria* L. f. (T, sp. 1), *Megistostigma* Hook. f. (Y, sp. 1), *Melanolepis* Rehb. (T, sp. 1), *Mercurialis* L. (Y, sp. 1; T, sp. 1), *Ostodes* Blume (Y, spp. 2), *Phyllanthodendron* Hemsl. (Y, spp. 4), *Phyllanthus* L. (Y, spp. 19; T, spp. 9), *Ricinus* L. (Y, sp. 1; T, sp. 1), *Sapium* Jacq. (Y, spp. 5; T, spp. 2), *Sauropus* Blume (Y, spp. 10), *Speranskia* Baill. (Y, spp. 2), *Strophoblachia* Boerl. (Y, sp. 1), *Sumbaviopsis* J. J. Sm. (Y, sp. 1), *Suregada* Roxb. (Y, sp. 1; T, sp. 1), *Synostemon* F. Muell. (T, sp. 1), *Trewia* L. (Y, sp. 1), *Trigonostemon* Blume (Y, spp. 4), *Vernicia* Lour. (Y, spp. 2).
- Eupteleaceae** (Y, gen. 1): *Euptelea* Sieb. & Zucc. (Y, sp. 1).
- Fabaceae** (Y, gen. 114; T, gen. 67): *Abarema* Pittier (Y, spp. 5), *Abrus* Adans. (Y, spp. 2; T, sp. 1), *Acacia* Mill. (Y, spp. 16; T, spp. 3), *Acrocarpus* Wight (Y, sp. 1), *Adenanthura* L. (Y, sp. 1), *Aeschynomene* L. (Y, sp. 1; T, spp. 2), *Afgekia* Craib (Y, sp. 1), *Albizia* Durazz. (Y, spp. 13; T, spp. 5), *Alysicarpus* Neck. (Y, spp. 5; T, spp. 4), *Amphicarpacea* Elliot (Y, spp. 3), *Antheroporum* Gagnep. (Y, spp. 2), *Apios* Fabr. (Y, spp. 4; T, sp. 1), *Archidendron* F. Muell. (T, sp. 1), *Astragalus* L. (Y, spp. 50; T, spp. 3), *Bauhinia* L. (Y, spp. 30; T, spp. 3), *Bowringia* Champ. (Y, sp. 1), *Butea* Roxb. (Y, spp. 2), *Caesalpinia* L. (Y, spp. 13; T, spp. 4), *Cajanus* Adans. (Y, spp. 7; T, spp. 2), *Callerya* Endl. (Y, spp. 9; T, spp. 2), *Calliandra* Benth. (Y, sp. 1), *Campylotropis* Bunge (Y, spp. 23; T, sp. 1), *Canavalia* Adans. (Y, spp. 3; T, spp. 4), *Caragana* Fabr. (Y, spp. 4), *Cassia* L. (Y, spp. 16), *Cercis* L. (Y, spp. 3), *Chamaecrista* Moench (T, spp. 3), *Chesneya* Lindl. ex Endl. (Y, spp. 3), *Christia* Moench (Y, spp. 2; T, spp. 2), *Cladrastis* Raf. (Y, spp. 3), *Clitoria* L. (Y, spp. 2; T, spp. 2), *Cochlianthus* Benth. (Y, spp. 2), *Codariocalyx* Hassk. (Y, spp. 2; T, sp. 1), *Colutea* L. (Y, sp. 1), *Craspedolobium* Harms (Y, sp. 1), *Crotalaria* L. (Y, spp. 25; T, spp. 19), *Cylindrokelupha* Kosterm. (Y, spp. 8), *Dalbergia* L. f. (Y, spp. 14; T, spp. 2), *Dendrolobium* (Wight & Arn.) Benth. (Y, sp. 1; T, spp. 3), *Derris* Lour. (Y, spp. 13; T, spp. 3), *Desmodium* Desv. (Y, spp. 30; T, spp. 15), *Dolichos* L. (Y, spp. 2), *Dumasia* DC. (Y, spp. 7; T, sp. 1), *Dunbaria* Wight & Arn. (Y, spp. 4; T, spp. 3), *Dysolobium* (Benth.) Prain (Y, sp. 1; T, sp. 1), *Entada* Adans. (Y, sp. 1; T, spp. 3), *Eriosema* (DC.) G. Don (Y, spp. 2; T, sp. 1), *Erythrina* L. (Y, spp. 7; T, sp. 1), *Erythrophleum* Afzel. (Y, sp. 1), *Euchresta* Benn. (Y, sp. 1; T, sp. 1), *Flemingia* Roxb. (Y, spp. 17; T, spp. 3), *Fordia* Hemsl. (Y, spp. 2), *Galactia* P. Browne (Y, spp. 2; T, spp. 2), *Gleditsia* L. (Y, spp. 2; T, sp. 1), *Glycine* Willd. (Y, spp. 2; T, spp. 3), *Glycyrrhiza* L. (Y, sp. 1), *Gueldenstaedtia* Fisch. (Y, spp. 3), *Gymnocladus* Lam. (Y, sp. 1), *Hedysarum* L. (Y, spp. 9), *Hylodesmum* H. Ohashi & R. Mill (Y, spp. 10; T, spp. 4), *Indigofera* L. (Y, spp. 48; T, spp. 15), *Kummerowia* Schindl. (Y, sp. 1; T, spp. 2), *Lablab* Adans. (Y, sp. 1; T, sp. 1), *Lathyrus* L. (Y, spp. 3), *Lespedeza* Michx. (Y, spp. 8; T, spp. 4), *Leucaena* Benth. (Y, sp. 1; T, sp. 1), *Lotus* L. (Y, sp. 1; T, sp. 1), *Lysidice*

- Hance (Y, sp. 1), *Maackia* Rupr. (T, sp. 1), *Macrotyloma* (Wight & Arn.) Verdc. (T, sp. 1), *Mecopus* Benn. (Y, sp. 1), *Medicago* L. (Y, spp. 2; T, spp. 3), *Melilotus* Mill. (Y, spp. 3; T, spp. 2), *Millettia* Wight & Arn. (Y, spp. 10; T, spp. 2), *Mimosa* L. (Y, spp. 2; T, spp. 3), *Mucuna* Adans. (Y, spp. 9; T, spp. 2), *Nogra* Merr. (Y, sp. 1), *Ohwia* H. Ohashi (T, sp. 1), *Ormocarpum* P. Beauv. (T, sp. 1), *Ormosia* Jacks. (Y, spp. 15; T, spp. 2), *Oxytropis* DC. (Y, spp. 3), *Parkia* R. Br. (Y, sp. 1), *Parochetus* Buch.-Ham. (Y, sp. 1), *Peltophorum* (Vogel) Benth. (Y, sp. 1), *Phaseolus* L. (Y, spp. 3), *Phylacium* Benn. (Y, sp. 1), *Phyllodium* Desv. (Y, spp. 4; T, sp. 1), *Piptanthus* (Hook.) D. Don (Y, spp. 2), *Pisum* L. (Y, sp. 1), *Pithecellobium* Mart. (Y, sp. 1), *Priotropis* Wight & Arn. (Y, sp. 1), *Psophocarpus* Neck. ex DC. (Y, sp. 1), *Pterocarpus* Jacq. (Y, spp. 2), *Pterolobium* R. Br. (Y, spp. 2), *Pueraria* DC. (Y, spp. 8; T, spp. 2), *Pycnospora* R. Br. (Y, sp. 1; T, sp. 1), *Rhynchosia* Lour. (Y, spp. 10; T, spp. 3), *Robinia* L. (Y, sp. 1), *Saraca* L. (Y, spp. 2), *Senna* Mill. (T, spp. 4), *Sesbania* Scop. (Y, spp. 3; T, spp. 2), *Shuteria* Wight & Arn. (Y, spp. 2), *Sindora* Miq. (Y, sp. 1), *Sinodolichos* Verdc. (Y, sp. 1), *Smithia* Aiton (Y, spp. 3; T, spp. 2), *Sophora* L. (Y, spp. 14; T, spp. 2), *Spatholobus* Hassk. (Y, spp. 8), *Tadehagi* H. Ohashi (Y, spp. 2), *Tamarindus* L. (Y, sp. 1), *Tephrosia* Pers. (Y, spp. 4; T, spp. 4), *Teramnus* P. Browne (T, sp. 1), *Thermopsis* R. Br. (Y, spp. 4), *Tibetia* (Ali) H. P. Tsui (Y, spp. 4), *Trifolium* L. (Y, spp. 2; T, spp. 3), *Trigonella* L. (Y, sp. 1; T, sp. 1), *Uraria* Desv. (Y, spp. 7; T, spp. 4), *Urariopsis* Schindl. (Y, spp. 2), *Vicia* L. (Y, spp. 15; T, spp. 3), *Vigna* Savi (Y, spp. 7; T, spp. 8), *Wisteria* Nutt. (Y, spp. 3), *Zenia* Chun (Y, sp. 1), *Zornia* J. F. Gmel. (Y, sp. 1; T, spp. 2).
- Fagaceae** (Y, gen. 7; T, gen. 8): *Castanea* Mill. (Y, spp. 3; T, spp. 2), *Castanopsis* (D. Don) Spach (Y, spp. 34; T, spp. 7), *Cyclobalanopsis* Oersted (Y, spp. 30; T, spp. 14), *Fagus* L. (Y, spp. 2; T, sp. 1), *Limlia* Masam. & Tomiya (T, sp. 1), *Lithocarpus* Blume (Y, spp. 44; T, spp. 2), *Pasania* Oerst. (T, spp. 12), *Quercus* L. (Y, spp. 28; T, spp. 9), *Trigonobalanus* Forman (Y, sp. 1).
- Flacourtiaceae** (Y, gen. 9; T, gen. 4): *Bennettiodendron* Merr. (Y, spp. 2), *Carrierea* Franch. (Y, spp. 2), *Flacourtia* Comm. (Y, spp. 4; T, sp. 1), *Gynocardia* R. Br. (Y, sp. 1), *Hydnocarpus* Gaertn. (Y, spp. 4), *Idesia* Maxim. (Y, sp. 1; T, sp. 1), *Itoa* Hemsl. (Y, sp. 1), *Scolopia* Schreb. (Y, sp. 1; T, sp. 1), *Xylosma* G. Forst. (Y, spp. 3; T, sp. 1).
- Flagellariaceae** (T, gen. 1): *Flagellaria* L. (T, sp. 1).
- Fumariaceae** (Y, gen. 4; T, gen. 2): *Corydalis* DC. (Y, spp. 72; T, spp. 8), *Dactylicapnos* Wall. (Y, spp. 4), *Dicentra* Borkh. (Y, spp. 2), *Fumaria* L. (T, sp. 1), *Hypecoum* L. (Y, sp. 1).
- Gentianaceae** (Y, gen. 17; T, gen. 6): *Canscora* Lam. (Y, sp. 1), *Centaurium* Hill (T, sp. 1), *Comastoma* (Wettst.) Toyokuni (Y, spp. 6), *Cotylanthera* Blume (Y, sp. 1), *Crawfurdia* Wall. (Y, spp. 8), *Exacum* L. (Y, spp. 2), *Gentiana* L. (Y, spp. 119; T, spp. 10), *Gentianella* Moench (Y, spp. 3), *Gentianopsis* Ma (Y, spp. 5), *Halenia* Borkh. (Y, sp. 1), *Latouchea* Franch. (Y, sp. 1), *Lomatogonium* A. Braun (Y, spp. 8; T, sp. 1), *Megacodon* (Hemsl.) Harry Sm. (Y, sp. 1), *Pterygocalyx* Maxim. (Y, sp. 1; T, sp. 1), *Sebaea* Sol. (Y, sp. 1), *Swertia* L. (Y, spp. 35; T, spp. 4), *Tripterispermum* Blume (Y, spp. 8; T, spp. 6), *Veratrilla* Baill. ex Franch. (Y, sp. 1).
- Geraniaceae** (Y, gen. 1; T, gen. 2): *Erodium* L'Hér. (T, spp. 2), *Geranium* L. (Y, spp. 29; T, spp. 5).
- Gesneriaceae** (Y, gen. 30; T, gen. 11): *Aeschynanthus* Jack (Y, spp. 31; T, sp. 1), *Ancylostemon* Craib (Y, spp. 6), *Anna* Pellegr. (Y, sp. 1), *Beccarinda* Kuntze (Y, spp. 5), *Boea* Comm. ex Lam. (Y, sp. 1), *Boeica* T. Anderson (Y, spp. 2), *Briggsia* Craib (Y, spp. 8), *Calcareoboea* C. Y. Wu (Y, sp. 1), *Chirita* Buch.-Ham. (Y, spp. 15; T, sp. 1), *Conandron* Sieb. & Zucc. (T, sp. 1), *Corallodiscus* Batalin (Y, spp. 11), *Cyrtandra* J. R. Forst. & G. Forst. (T, sp. 1), *Didissandra* C. B. Clarke (Y, spp. 2), *Didymocarpus* Wall. (Y, spp. 15), *Epithema* Blume (Y, sp. 1; T, sp. 1), *Hemiboea* C. B. Clarke (Y, spp. 8; T, sp. 1), *Hemiboeopsis* W. T. Wang (Y, sp. 1), *Lagarosolen* W. T. Wang (Y, sp. 1), *Leptoboea* Benth. (Y, sp. 1), *Loxostigma* C. B. Clarke (Y, spp. 7), *Lysionotus* D. Don (Y, spp. 17; T, sp. 1), *Oreocharis* Benth. (Y, spp. 14), *Ornithoboea* Parish (Y, spp. 4), *Paraboea* (C. B. Clarke) Ridl. (Y, spp. 5; T, sp. 1), *Petrocosmea* Oliv. (Y, spp. 20), *Rhabdothamnopsis* Hemsl. (Y, sp. 1), *Rhynchoglossum* Blume (Y, sp. 1), *Rhynchotechum* Blume (Y, spp. 3; T, spp. 4), *Stauranthera* Benth. (Y, spp. 2), *Titanotrichum* Soler. (T, sp. 1), *Tremacron* Craib (Y, spp. 4), *Trisepalum* C. B. Clarke (Y, sp. 1), *Whytockia* W. W. Sm. (Y, spp. 5; T, sp. 1).
- Ginkgoaceae** (Y, gen. 1): *Ginkgo* L. (Y, sp. 1).
- Gnetaceae** (Y, gen. 1): *Gnetum* L. (Y, spp. 4).
- Goodeniaceae** (T, gen. 1): *Scaevola* L. (T, spp. 2).
- Grossulariaceae** (Y, gen. 1; T, gen. 1): *Ribes* L. (Y, spp. 16; T, sp. 1).
- Haloragaceae** (Y, gen. 2; T, gen. 2): *Haloragis* J. R. Forst. & G. Forst. (Y, spp. 2; T, sp. 1), *Myriophyllum* L. (Y, spp. 2; T, spp. 4).
- Hamamelidaceae** (Y, gen. 11; T, gen. 6): *Altingia* Noronha (Y, spp. 4), *Corylopsis* Sieb. & Zucc. (Y, spp. 9; T, spp. 2), *Distyliopsis* Endress (Y, spp. 3; T, sp. 1), *Distylium* Sieb. & Zucc. (Y, spp. 4; T, spp. 2), *Eustigma* Gardn. & Champ. (Y, spp. 2; T, sp. 1), *Liquidambar* L. (Y, sp. 1; T, sp. 1), *Loropetalum* R. Br. ex Rehb. (Y, spp. 2), *Mytilaria* Lecomte (Y, sp. 1), *Rhodoleia* Champ. (Y, spp. 3), *Sycopsis* Oliv. (Y, spp. 2; T, sp. 1), *Exbucklandia* R. W. Brown (Y, spp. 2).
- Hernandiaceae** (Y, gen. 1; T, gen. 2): *Hernandia* L. (T, sp. 1), *Illigera* Blume (Y, spp. 11; T, sp. 1).
- Hippocastanaceae** (Y, gen. 1): *Aesculus* L. (Y, spp. 5).
- Hydrangeaceae** (Y, gen. 6; T, gen. 4): *Deutzia* Thunb. (Y, spp. 21; T, spp. 3), *Dichroa* Lour. (Y, spp. 4), *Hydrangea* L. (Y, spp. 18; T, spp. 7), *Philadelphus* L. (Y, spp. 10), *Pileostegia* Hook. f. & Thomson (Y, sp. 1; T, sp. 1), *Schizophragma* Sieb. & Zucc. (Y, spp. 4; T, sp. 1).
- Hydrocharitaceae** (Y, gen. 6; T, gen. 8): *Blyxa* Noronha (Y, spp. 4; T, spp. 3), *Halophila* Thouars (T, spp. 3), *Hydrilla* Rich. (Y, sp. 1; T, sp. 1), *Hydrocharis* L. (Y, sp. 1; T, sp. 1), *Najas* L. (Y, spp. 4; T, spp. 7), *Ottelia* Pers. (Y, spp. 2; T, sp. 1), *Thalassia* Banks (T, sp. 1), *Vallisneria* L. (Y, sp. 1; T, sp. 1).
- Hydrophyllaceae** (Y, gen. 1; T, gen. 1): *Hydrolea* L. (Y, sp. 1; T, sp. 1).
- Hypericaceae** (Y, gen. 3; T, gen. 2): *Cratoxylum* Blume (Y, spp. 2), *Hypericum* L. (Y, spp. 27; T, spp. 14), *Triadenum* Raf. (Y, sp. 1; T, sp. 1).
- Hypoxidaceae** (Y, gen. 2; T, gen. 3): *Curculigo* Gaertn. (Y, spp. 4; T, spp. 2), *Hypoxis* L. (Y, sp. 1; T, sp. 1), *Molineria* Colla (T, sp. 1).
- Icacinaceae** (Y, gen. 10; T, gen. 3): *Apodytes* E. Mey. (Y, sp. 1), *Gomphandra* Wall. (Y, spp. 2; T, sp. 1), *Gonocaryum* Miq. (Y, sp. 1; T, sp. 1), *Iodes* Blume (Y, spp. 4), *Mappianthus* Hand.-Mazz. (Y, sp. 1), *Natsiatopsis* Kurz (Y, sp. 1), *Natsiatum* Buch.-Ham. (Y, sp. 1), *Nothapodytes* Blume (Y, spp. 3; T, sp. 1), *Pittosporopsis* Craib (Y, sp. 1), *Platea* Blume (Y, sp. 1).
- Iridaceae** (Y, gen. 4; T, gen. 3): *Belamcanda* Adans. (Y, sp. 1; T, sp. 1), *Crocus* L. (Y, sp. 1), *Iris* L. (Y, spp. 23; T, spp. 2), *Sisyrinchium* L. (Y, sp. 1; T, spp. 2).
- Iteaceae** (Y, gen. 1; T, gen. 1): *Itea* L. (Y, spp. 7; T, spp. 2).

Ixonanthaceae (Y, gen. 1): *Ixonanthes* Jack (Y, spp. 2).

Juglandaceae (Y, gen. 8; T, gen. 3): *Annamocarya* A. Chev. (Y, sp. 1), *Carya* Nutt. (Y, sp. 1), *Cyclocarya* Iljinsk. (Y, sp. 1), *Engelhardtia* Leschen. (Y, spp. 5; T, sp. 1), *Juglans* L. (Y, spp. 4; T, sp. 1), *Platycarya* Sieb. & Zucc. (Y, spp. 2; T, sp. 1), *Pterocarya* Kunth (Y, spp. 3), *Rhoiptelea* Diels & Handl.-Mazz. (Y, sp. 1).

Juncaceae (Y, gen. 2; T, gen. 2): *Juncus* L. (Y, spp. 51; T, spp. 5), *Luzula* DC. (Y, spp. 7; T, spp. 4).

Juncaginaceae (Y, gen. 1): *Triglochin* L. (Y, spp. 2).

Lamiaceae (Y, gen. 78; T, gen. 41): *Acrocephalus* Benth. (Y, sp. 1; T, sp. 1), *Agastache* J. Clayton. (Y, sp. 1; T, sp. 1), *Ajuga* L. (Y, spp. 12; T, spp. 5), *Amethystea* L. (Y, sp. 1), *Anisochilus* Wall. (Y, sp. 1), *Anisomeles* R. Br. (T, sp. 1), *Basilicum* Moench (T, sp. 1), *Bostrychanthera* Benth. (T, sp. 1), *Callicarpa* L. (Y, spp. 14; T, spp. 9), *Cardioteucris* C. Y. Wu (Y, sp. 1), *Caryopteris* Bunge (Y, spp. 9; T, sp. 1), *Ceratanthus* F. Muell. (Y, sp. 1), *Chelonopsis* Miq. (Y, spp. 8), *Clerodendranthus* Kudô (Y, sp. 1), *Clerodendrum* L. (Y, spp. 25; T, spp. 7), *Clinopodium* L. (Y, spp. 6; T, spp. 3), *Colebrookea* Sm. (Y, sp. 1), *Coleus* Lour. (Y, spp. 5; T, spp. 2), *Colquhounia* Wall. (Y, spp. 5), *Comanthosphace* S. Moore (T, sp. 1), *Congea* Roxb. (Y, spp. 2), *Craniotome* Rchb. (Y, sp. 1), *Dracocephalum* L. (Y, spp. 8), *Dysophylla* Blume (Y, spp. 5), *Elsholtzia* Willd. (Y, spp. 26; T, spp. 2), *Epimeredi* Adans. (Y, sp. 1), *Eriophyton* Benth. (Y, sp. 1), *Eurysolen* Prain (Y, sp. 1), *Galeopsis* L. (Y, sp. 1), *Garrettia* H. R. Fletcher (Y, sp. 1), *Geniosporum* Wall. (Y, sp. 1), *Glechoma* L. (Y, spp. 2), *Gmelina* L. (Y, spp. 3), *Gomphostemma* Wall. (Y, spp. 10; T, sp. 1), *Hanceola* Kudô (Y, spp. 2), *Heterolamium* C. Y. Wu (Y, sp. 1), *Holocheila* (Kudo) S. Chow ex C. Y. Wu & S. Ch (Y, sp. 1), *Hyptis* Jacq. (T, spp. 4), *Isodon* (Schrud.) Spach (T, spp. 3), *Keiskea* Miq. (Y, sp. 1; T, sp. 1), *Kinostemon* Kudô (Y, sp. 1), *Lagopsis* Bunge (Y, sp. 1), *Lamiophlomis* Kudô (Y, sp. 1), *Lamium* L. (Y, sp. 1; T, spp. 2), *Leonurus* L. (Y, sp. 1; T, sp. 1), *Leucas* R. Br. (Y, spp. 4; T, sp. 1), *Leucosceptrum* Sm. (Y, sp. 1), *Loxocalyx* Hemsl. (Y, sp. 1), *Lycopus* L. (Y, spp. 2; T, sp. 1), *Maesa* Forssk. (Y, spp. 19; T, spp. 3), *Meehanina* Britt. (Y, sp. 1), *Melissa* L. (Y, spp. 2; T, sp. 1), *Mentha* L. (Y, spp. 4; T, sp. 1), *Mesona* Blume (Y, sp. 1; T, sp. 1), *Micromeria* Benth. (Y, spp. 3), *Microtoena* Prain (Y, spp. 10), *Mosla* (Benth.) Buch.-Ham. (Y, spp. 2; T, spp. 3), *Nepeta* L. (Y, spp. 8), *Notochaete* Benth. (Y, spp. 2), *Ocimum* L. (Y, spp. 3; T, spp. 3), *Origanum* L. (Y, sp. 1; T, sp. 1), *Orthosiphon* Benth. (Y, sp. 1; T, sp. 1), *Paralamium* Dunn (Y, sp. 1), *Paraphlomis* Prain (Y, spp. 4; T, spp. 3), *Perilla* L. (Y, sp. 1; T, sp. 1), *Phlomis* L. (Y, spp. 16), *Phyllophyton* Kudô (Y, sp. 1), *Pogostemon* Desf. (Y, spp. 12; T, spp. 3), *Premna* L. (Y, spp. 27; T, spp. 5), *Prunella* L. (Y, spp. 2), *Rabdosia* (Blume) Hasskarl (Y, spp. 47), *Rostrinucula* Kudô (Y, sp. 1), *Rubiteucris* Kudô (Y, sp. 1; T, sp. 1), *Salvia* L. (Y, spp. 37; T, spp. 9), *Schizonepeta* Briq. (Y, sp. 1), *Schnabelia* Handl.-Mazz. (Y, sp. 1), *Scutellaria* L. (Y, spp. 33; T, spp. 6), *Siphocranion* Kudô (Y, spp. 2), *Skapanthus* C. Y. Wu & H. W. Li (Y, sp. 1), *Sphenodesme* Jack (Y, spp. 2; T, sp. 1), *Stachys* L. (Y, spp. 5; T, spp. 2), *Suzukia* Kudô (T, spp. 2), *Symphorema* Roxb. (Y, sp. 1), *Teucrium* L. (Y, spp. 10; T, spp. 3), *Vitex* L. (Y, spp. 10; T, spp. 4).

Lardizabalaceae (Y, gen. 5; T, gen. 2): *Akebia* Decne. (Y, sp. 1; T, sp. 1), *Decaisnea* Hook. f. & Thomson (Y, sp. 1), *Holboellia* Wall. (Y, spp. 5), *Sinofranchetia* Hemsl. (Y, sp. 1), *Stauntonia* DC. (Y, spp. 6; T, spp. 3).

Lauraceae (Y, gen. 16; T, gen. 12): *Actinodaphne* Nees (Y, spp. 7), *Alseodaphne* Nees (Y, spp. 7), *Beilschmiedia* Nees (Y, spp. 17; T, spp. 2), *Caryodaphnopsis* Airy Shaw (Y, spp.

4), *Cassytha* L. (Y, sp. 1; T, sp. 1), *Cinnamomum* Schaeffer (Y, spp. 26; T, spp. 14), *Cryptocarya* R. Br. (Y, spp. 8; T, spp. 3), *Dehaasia* Blume (T, sp. 1), *Endiandra* R. Br. (T, sp. 1), *Lindera* Thunb. (Y, spp. 21; T, spp. 7), *Litsea* Lam. (Y, spp. 43; T, spp. 10), *Machilus* Nees (Y, spp. 23; T, spp. 6), *Neocinnamomum* H. Liou (Y, spp. 4), *Neolitsea* Merr. (Y, spp. 16; T, spp. 10), *Nothaphoebe* Blume (Y, sp. 1), *Phoebe* Nees (Y, spp. 21; T, sp. 1), *Sassafras* T. Nees & C. H. Eberm. (Y, sp. 1; T, sp. 1), *Syndiclis* Hook. f. (Y, spp. 5).

Lecythydaceae (Y, gen. 1; T, gen. 1): *Barringtonia* J. R. Forst. & G. Forst. (Y, spp. 2; T, spp. 2).

Lemnaceae (Y, gen. 3; T, gen. 3): *Lemna* L. (Y, spp. 3; T, spp. 2), *Spirodela* Schleid. (Y, sp. 1; T, spp. 2), *Wolffia* Horkel (Y, sp. 1; T, sp. 1).

Lentibulariaceae (Y, gen. 2; T, gen. 1): *Pinguicula* L. (Y, sp. 1), *Utricularia* L. (Y, spp. 9; T, spp. 8).

Liliaceae (Y, gen. 36; T, gen. 20): *Alettris* L. (Y, spp. 8; T, spp. 2), *Aloe* L. (Y, sp. 1), *Aspidistra* Ker Gawl. (Y, 4 spp.; T, sp. 1), *Barnardia* Lindl. (T, sp. 1), *Campylandra* Baker (T, sp. 1), *Cardiocrinum* (Endl.) Lindl. (Y, sp. 1), *Chlorophytum* Ker-Gawl. (Y, spp. 4), *Clintonia* Raf. (Y, sp. 1), *Dianella* Lam. (Y, sp. 1; T, sp. 1), *Disporopsis* Hance (Y, spp. 4; T, sp. 1), *Disporum* Salisb. (Y, spp. 7; T, spp. 4), *Diurandthera* Hemsl. (Y, sp. 1), *Eremurus* M. Bieb. (Y, sp. 1), *Fritillaria* L. (Y, spp. 4), *Gloriosa* L. (Y, sp. 1), *Helonias* L. (T, sp. 1), *Hemerocallis* L. (Y, spp. 5; T, sp. 1), *Hosta* Tratt. (Y, spp. 2), *Iphigenia* Kunth (Y, sp. 1), *Lilium* L. (Y, spp. 23; T, spp. 2), *Liriope* Lour. (Y, spp. 3; T, spp. 2), *Lloydia* Rchb. (Y, spp. 6), *Maianthemum* F. H. Wigg. (Y, spp. 12), *Nomocharis* Franch. (Y, spp. 7), *Notholirion* Wall. (Y, spp. 3), *Ophiopogon* Ker Gawl. (Y, spp. 33; T, spp. 2), *Peliosanthes* Andrews (Y, spp. 7; T, sp. 1), *Petrosavia* Becc. (Y, sp. 1; T, sp. 1), *Polygonatum* Mill. (Y, spp. 10; T, spp. 2), *Reineckea* Kunth (Y, sp. 1), *Rohdea* Roth (Y, sp. 1), *Scilla* L. (Y, sp. 1; T, sp. 1), *Smilacina* Desf. (T, sp. 1), *Streptopus* Michx. (Y, spp. 3), *Theropogon* Maxim. (Y, sp. 1), *Thysanotus* R. Br. (T, sp. 1), *Tofieldia* Huds. (Y, spp. 2), *Tricyrtis* Wall. (Y, sp. 1; T, spp. 2), *Tupistra* Ker Gawl. (Y, spp. 11), *Veratrum* L. (Y, spp. 6; T, spp. 2), *Ypsilandra* Franch. (Y, spp. 3).

Linaceae (Y, gen. 4): *Anisadenia* Wall. (Y, spp. 2), *Linum* L. (Y, spp. 2), *Reinwardtia* Dumort. (Y, sp. 1), *Tirpitzia* Hallier f. (Y, sp. 1).

Linderniaceae (Y, gen. 2; T, gen. 2): *Lindernia* All. (Y, spp. 14; T, spp. 15), *Torenia* L. (Y, spp. 6; T, spp. 4).

Loganiaceae (Y, gen. 7; T, gen. 6): *Buddleja* L. (Y, spp. 23; T, spp. 2), *Fagraea* Thunb. (Y, sp. 1; T, sp. 1), *Gardneria* Wall. (Y, spp. 6; T, spp. 2), *Gelsemium* Juss. (Y, sp. 1), *Geniostoma* J. R. Forst. & G. Forst. (T, sp. 1), *Mitrasacme* Labill. (Y, sp. 1; T, spp. 2), *Mitreola* L. (Y, spp. 3), *Strychnos* L. (Y, spp. 4; T, sp. 1).

Loranthaceae (Y, gen. 10; T, gen. 4): *Arceuthobium* M. Bieb. (Y, spp. 2), *Dendrophthoe* Mart. (Y, sp. 1), *Elytranthe* (Blume) Blume (Y, spp. 2), *Helixanthera* Lour. (Y, spp. 5), *Korthalsella* Tiegh. (Y, sp. 1; T, sp. 1), *Loranthus* Jacq. (Y, sp. 1; T, spp. 2), *Macrosolen* (Bl.) Reichb. (Y, spp. 2), *Scurrula* L. (Y, spp. 7), *Taxillus* Tiegh. (Y, spp. 9; T, spp. 10), *Viscum* L. (Y, spp. 9; T, spp. 4).

Lythraceae (Y, gen. 7; T, gen. 5): *Ammannia* L. (Y, spp. 3; T, spp. 3), *Lagerstroemia* L. (Y, spp. 7; T, sp. 1), *Lawsonia* L. (Y, sp. 1), *Lythrum* L. (Y, sp. 1), *Pemphis* J. R. Forst. & G. Forst. (T, sp. 1), *Rotala* L. (Y, spp. 5; T, spp. 6), *Trapa* L. (Y, spp. 3; T, sp. 1), *Woodfordia* Salisb. (Y, sp. 1).

Magnoliaceae (Y, gen. 12; T, gen. 2): *Alcimandra* Dandy (Y, sp. 1), *Liriodendron* L. (Y, spp. 2), *Magnolia* L. (Y, spp. 10; T, sp. 1), *Manglietia* Blume (Y, spp. 16), *Manglietiastrum* Y. W. Law (Y, sp. 1), *Michelia* L. (Y, spp. 23; T, sp. 1),

Parakmeria Hu & W. C. Cheng (Y, spp. 2), *Paramichelia* Hu (Y, sp. 1), *Talauma* Juss. (Y, sp. 1), *Tsoongiodendron* Chun (Y, sp. 1), *Woonyoungia* Law (Y, sp. 1), *Yulania* Spach (Y, spp. 6).

Malpighiaceae (Y, gen. 2; T, gen. 3): *Aspidopterys* Juss. (Y, spp. 6), *Hiptage* Gaertn. (Y, spp. 6; T, sp. 1), *Ryssopterys* Blume (T, sp. 1), *Tristellateia* Thouars (T, sp. 1).

Malvaceae (Y, gen. 11; T, gen. 8): *Abelmoschus* Medik. (Y, spp. 5; T, sp. 1), *Abutilon* Mill. (Y, spp. 8; T, spp. 3), *Althaea* L. (Y, sp. 1), *Cenocentrum* Gagnep. (Y, sp. 1), *Hibiscus* L. (Y, spp. 14; T, spp. 5), *Kydia* Roxb. (Y, spp. 3), *Malva* L. (Y, spp. 4; T, spp. 2), *Malvastrum* A. Gray (Y, sp. 1; T, spp. 2), *Sida* L. (Y, spp. 11; T, spp. 7), *Thespesia* Sol. (Y, sp. 1; T, sp. 1), *Urena* L. (Y, spp. 3; T, spp. 2).

Marantaceae (Y, gen. 3; T, gen. 1): *Donax* Lour. (Y, sp. 1; T, sp. 1), *Phrynium* Willd. (Y, spp. 3), *Stachyphrynium* K. Schum (Y, sp. 1).

Martyniaceae (Y, gen. 1): *Martynia* L. (Y, sp. 1).

Melastomataceae (Y, gen. 17; T, gen. 12): *Allomorphia* Blume (Y, spp. 4), *Astronia* Blume (T, sp. 1), *Barthea* Hook. f. (T, sp. 1), *Blastus* Lour. (Y, spp. 4; T, sp. 1), *Bredia* Blume (Y, spp. 5; T, spp. 2), *Cyphotheca* Diels. (Y, sp. 1), *Fordiophyton* Stapf (Y, spp. 4), *Medinilla* Gaudich. (Y, spp. 10; T, spp. 2), *Melastoma* L. (Y, spp. 4; T, spp. 3), *Memecylon* L. (Y, spp. 4; T, sp. 1), *Osbeckia* L. (Y, spp. 10; T, spp. 2), *Otanthera* Blume (T, sp. 1), *Oxyspora* DC. (Y, spp. 3), *Pachycentria* Blume (T, sp. 1), *Phyllagathis* Blume (Y, spp. 6), *Plagiopetalum* Rehder (Y, spp. 3), *Sarcopyramis* Wall. (Y, spp. 3; T, sp. 1), *Sonerila* Roxb. (Y, spp. 7; T, sp. 1), *Sporoxeia* W. W. Sm. (Y, spp. 3), *Stapfiophyton* H. L. Li (Y, sp. 1), *Styrophyton* S. Y. Hu (Y, sp. 1).

Meliaceae (Y, gen. 12; T, gen. 5): *Aglaia* Lour. (Y, spp. 4; T, spp. 3), *Amoora* Roxb. (Y, spp. 7), *Aphanamixis* Blume (Y, spp. 3; T, sp. 1), *Chisocheton* Blume (Y, spp. 2; T, sp. 1), *Chukrasia* A. Juss. (Y, sp. 1), *Cipadessa* Blume (Y, spp. 2), *Dysoxylum* Blume (Y, spp. 10; T, spp. 4), *Melia* L. (Y, spp. 2; T, sp. 1), *Munronia* Wight (Y, spp. 3), *Toona* (Endl.) Roem. (Y, spp. 3), *Trichilia* P. Browne (Y, sp. 1), *Walsura* Roxb. (Y, spp. 2).

Menispermaceae (Y, gen. 16; T, gen. 6): *Albertisia* Becc. (Y, sp. 1), *Aspidocarya* Hook. f. & Thomson (Y, sp. 1), *Cissampelos* L. (Y, sp. 1), *Cocculus* DC. (Y, spp. 2; T, spp. 2), *Cyclea* Arn. (Y, spp. 7; T, spp. 3), *Diploclisia* Miers. (Y, spp. 2), *Eleutharrhena* Forman (Y, sp. 1), *Fibraurea* Lour. (Y, sp. 1), *Hypserpa* Miers (Y, sp. 1), *Parabaena* Miers (Y, sp. 1), *Pericampylus* Miers (Y, sp. 1; T, sp. 1), *Pycnarrhena* Miers (Y, sp. 1), *Sinomenium* Diels (Y, sp. 1; T, sp. 1), *Stephania* Lour. (Y, spp. 17; T, spp. 4), *Tinomiscium* Miers (Y, sp. 1), *Tinospora* Miers (Y, spp. 3; T, sp. 1).

Menyanthaceae (Y, gen. 2; T, gen. 1): *Menyanthes* L. (Y, sp. 1), *Nymphoides* Hill (Y, spp. 2; T, spp. 6).

Mitrastemonaceae (Y, gen. 1; T, gen. 1): *Mitrastemon* Makino (Y, sp. 1; T, spp. 2).

Molluginaceae (Y, gen. 2; T, gen. 2): *Glinus* L. (Y, spp. 2; T, spp. 2), *Mollugo* L. (Y, sp. 1; T, spp. 2).

Moraceae (Y, gen. 8; T, gen. 6): *Antiaris* Lesch. (Y, sp. 1), *Artocarpus* J. R. Forst. & G. Forst. (Y, spp. 12; T, spp. 2), *Broussonetia* L'Hér. (Y, spp. 4; T, spp. 3), *Cudrania* Trécul (Y, spp. 5), *Fatoua* Gaudich. (Y, sp. 1; T, spp. 2), *Ficus* L. (Y, spp. 66; T, spp. 22), *Machura* Nutt. (T, sp. 1), *Morus* L. (Y, spp. 8; T, sp. 1), *Streblus* Lour. (Y, spp. 6).

Musaceae (Y, gen. 3; T, gen. 1): *Ensete* Bruce (Y, sp. 1), *Musa* L. (Y, spp. 8; T, sp. 1), *Musella* (Fr.) C. Y. Wu (Y, sp. 1).

Myricaceae (Y, gen. 1; T, gen. 1): *Myrica* L. (Y, spp. 3; T, spp. 2).

Myristicaceae (Y, gen. 3): *Horsfieldia* Willd. (Y, spp. 4), *Knema* Lour. (Y, spp. 5), *Myristica* Gronov. (Y, sp. 1).

Myrsinaceae (Y, gen. 4; T, gen. 3): *Ardisia* Sw. (Y, spp. 36; T, spp. 15), *Embelia* Burm. f. (Y, spp. 18; T, spp. 2), *Myrsine* L. (Y, spp. 3; T, spp. 3), *Rapanea* Aubl. (Y, spp. 6).

Myrtaceae (Y, gen. 4; T, gen. 4): *Acmena* DC. (T, sp. 1), *Cleistocalyx* Blume (Y, sp. 1), *Decaspermum* J. R. Forst. & G. Forst. (Y, sp. 1; T, sp. 1), *Rhodomyrtus* (DC.) Reichenbach (Y, sp. 1; T, sp. 1), *Syzygium* R. Br. (Y, spp. 34; T, spp. 8).

Nelumbonaceae (Y, gen. 1; T, gen. 1): *Nelumbo* Adans. (Y, sp. 1; T, sp. 1).

Nyctaginaceae (Y, gen. 3; T, gen. 2): *Boerhavia* L. (Y, sp. 1; T, sp. 1), *Commicarpus* Standl. (Y, sp. 1), *Pisonia* L. (Y, sp. 1; T, spp. 2).

Nymphaeaceae (Y, gen. 2; T, gen. 3): *Euryale* Salisb. (T, sp. 1), *Nuphar* Sm. (Y, spp. 2; T, sp. 1), *Nymphaea* L. (Y, spp. 4; T, spp. 2).

Nyssaceae (Y, gen. 2): *Camptotheca* Decne. (Y, sp. 1), *Nyssa* Gronov. (Y, spp. 4).

Olacaceae (Y, gen. 2; T, gen. 1): *Malania* Chun & S. K. Lee (Y, sp. 1), *Olax* L. (Y, sp. 1; T, sp. 1).

Oleaceae (Y, gen. 11; T, gen. 5): *Chionanthus* L. (Y, sp. 1; T, spp. 3), *Erythralum* Blume (Y, sp. 1), *Fontanesia* Labill. (Y, sp. 1), *Forsythia* Vahl (Y, spp. 3), *Fraxinus* L. (Y, spp. 12; T, spp. 2), *Jasminum* L. (Y, spp. 30; T, spp. 4), *Ligustrum* L. (Y, spp. 13; T, spp. 4), *Linociera* Sw. (Y, spp. 4), *Olea* L. (Y, spp. 9), *Osmanthus* Lour. (Y, spp. 10; T, spp. 6), *Syringa* L. (Y, spp. 6).

Onagraceae (Y, gen. 4; T, gen. 3): *Chamaenerion* Seguiet (Y, spp. 2), *Circaea* L. (Y, spp. 8; T, spp. 3), *Epilobium* L. (Y, spp. 17; T, spp. 6), *Ludwigia* L. (Y, spp. 5; T, spp. 7).

Opiliaceae (Y, gen. 5; T, gen. 1): *Cansjera* Juss. (Y, sp. 1), *Champereia* Griff. (T, sp. 1), *Lepionurus* Blume (Y, sp. 1), *Melientha* Pierre (Y, sp. 1), *Opilia* Roxb. (Y, sp. 1), *Urobotrya* Stapf (Y, sp. 1).

Orchidaceae (Y, gen. 136; T, gen. 104): *Acampe* Lindl. (Y, spp. 3; T, sp. 1), *Acanthephippium* Blume (Y, spp. 2; T, spp. 2), *Acriopsis* Reinw. (Y, sp. 1), *Aerides* Lour. (Y, spp. 4), *Agrostophyllum* Blume (Y, sp. 1; T, sp. 1), *Amitostigma* Schltr. (Y, spp. 10; T, spp. 2), *Androcorys* Schltr. (Y, spp. 3; T, sp. 1), *Ania* Lindl. (T, sp. 1), *Anoetochilus* Blume (Y, spp. 12; T, spp. 2), *Anthogonium* Wall. (Y, sp. 1), *Aphyllorchis* Blume (Y, spp. 2; T, sp. 1), *Apostasia* Blume (Y, spp. 2), *Appendicula* Blume (T, spp. 2), *Arachnis* Blume (Y, sp. 1; T, sp. 1), *Arundina* Blume (Y, sp. 1; T, sp. 1), *Ascocentrum* Schltr. (Y, spp. 2; T, sp. 1), *Bletilla* Rehb. f. (Y, spp. 3; T, spp. 2), *Brachycorythis* Lindl. (Y, spp. 2; T, sp. 1), *Bulbophyllum* Thouars (Y, spp. 65; T, spp. 24), *Bulleyia* Schltr. (Y, sp. 1), *Calanthe* Ker Gawl. (Y, spp. 27; T, spp. 19), *Calypso* Salisb. (Y, sp. 1), *Cephalanthera* Rich. (Y, spp. 4; T, sp. 1), *Cephalantheropsis* Guillaumin (Y, spp. 2; T, spp. 3), *Ceratostylis* Blume (Y, sp. 1), *Chamaegastrodia* Makino & F. Maek. (Y, spp. 2), *Cheirostylis* Blume (Y, spp. 3; T, spp. 8), *Chiloschista* Lindl. (Y, sp. 1; T, sp. 1), *Chrysoglossum* Blume (Y, sp. 1; T, sp. 1), *Cleisostoma* Blume (Y, spp. 12; T, spp. 2), *Coeloglossum* Hartm. (Y, sp. 1; T, sp. 1), *Coelogyne* Lindl. (Y, spp. 23), *Collabium* Blume (Y, spp. 3; T, spp. 2), *Corybas* Salisb. (Y, sp. 1; T, spp. 2), *Corymborkis* Thouars (Y, sp. 1), *Cremastra* Lindl. (Y, sp. 1; T, sp. 1), *Cryptochilus* Wall. (Y, spp. 2), *Cryptostylis* R. Br. (T, spp. 2), *Cymbidium* Sw. (Y, spp. 28; T, spp. 9), *Cypripedium* L. (Y, spp. 15; T, spp. 4), *Cyrtosia* Blume (T, sp. 1), *Dendrobium* Sw. (Y, spp. 59; T, spp. 12), *Dendrochilum* Blume (T, sp. 1), *Didiciea* King & Prain (T, sp. 1), *Didymoplexiella* Garay (T, sp. 1), *Didymoplexis* Griff. (T, sp. 1), *Diglyphosa* Blume (Y, sp. 1), *Diphylax* Hook. f. (Y, spp. 3), *Diplomeris* D. Don (Y, sp. 1), *Diploprora* Hook. f. (Y, sp. 1; T, sp. 1), *Disperis* Sw. (T, sp. 1), *Epigeneium*

- Gagnep. (Y, spp. 6; T, spp. 2), *Epipactis* Zinn. (Y, spp. 3), *Epipogium* Gmelin (Y, spp. 2; T, spp. 2), *Eria* Lindl. (Y, spp. 30; T, spp. 7), *Eriodes* Rolfe (Y, sp. 1), *Erythroides* Blume (Y, sp. 1; T, sp. 1), *Erythrorchis* Blume (T, sp. 1), *Esmeralda* Rchb. f. (Y, spp. 2), *Eulophia* R. Br. (Y, spp. 7; T, spp. 4), *Flickingeria* A. D. Hawkes (Y, spp. 6; T, spp. 2), *Galeola* Lour. (Y, spp. 2; T, spp. 2), *Gastrochilus* D. Don (Y, spp. 12; T, spp. 9), *Gastrodia* R. Br. (Y, spp. 4; T, spp. 9), *Geodorum* G. Jacks. (Y, spp. 4; T, sp. 1), *Goodyera* R. Br. (Y, spp. 16; T, spp. 20), *Gymnadenia* R. Br. (Y, spp. 3; T, spp. 4), *Habenaria* Willd. (Y, spp. 35; T, spp. 8), *Hancockia* Rolfe (Y, sp. 1), *Haraella* Kudô (T, sp. 1), *Hemipilia* Lindl. (Y, spp. 4; T, sp. 1), *Herminium* L. (Y, spp. 16; T, sp. 1), *Herpysma* Lindl. (Y, sp. 1), *Hetaeria* Blume (Y, sp. 1; T, sp. 1), *Holcoglossum* Schltr. (Y, spp. 7; T, sp. 1), *Hygrochilus* Pfitz. (Y, sp. 1), *Hylophila* Lindl. (T, sp. 1), *Kingidium* P. F. Hunt (Y, spp. 3), *Lecanorchis* Blume (Y, sp. 1; T, spp. 3), *Liparis* Rich. (Y, spp. 35; T, spp. 20), *Listera* R. Br. (Y, spp. 5; T, spp. 9), *Ludisia* A. Rich. (Y, sp. 1), *Luisia* Gaudich. (Y, spp. 7; T, spp. 3), *Malaxis* Sol. (Y, spp. 12; T, spp. 7), *Malleola* J. J. Sm. & Schltr. (Y, sp. 1), *Microtatorchis* Schltr. (T, sp. 1), *Microtis* R. Br. (T, sp. 1), *Mischobulbum* Schltr. (Y, sp. 1; T, sp. 1), *Monomeria* Lindl. (Y, sp. 1), *Myrmechis* Blume (Y, spp. 3; T, sp. 1), *Neogyna* Rchb. f. (Y, sp. 1), *Neottia* Guett. (Y, spp. 4; T, sp. 1), *Neottianthe* Schltr. (Y, spp. 7), *Nervilia* Comm. (Y, spp. 3; T, spp. 5), *Neuwiedia* Blume (Y, sp. 1), *Oberonia* Lindl. (Y, spp. 18; T, spp. 7), *Odontochilus* Blume (T, spp. 4), *Orchis* L. (Y, spp. 11), *Oreorchis* Lindl. (Y, spp. 7; T, spp. 4), *Ornithochilus* (Lindl.) Wall. (Y, spp. 2), *Otochilus* Lindl. (Y, spp. 4), *Pachystoma* Blume (Y, sp. 1; T, sp. 1), *Panisea* (Lindl.) Steud. (Y, spp. 4), *Paphiopedilum* Pfitz. (Y, spp. 14), *Papilionanthe* Schltr. (Y, spp. 2; T, sp. 1), *Parapteroceras* Averyanov (Y, sp. 1), *Pecteilis* Raf. (Y, spp. 2), *Pelatantheria* Ridl. (Y, spp. 3), *Pennilabium* J. J. Sm. (Y, sp. 1), *Peristylus* Blume (Y, spp. 15; T, spp. 4), *Phaius* Lour. (Y, spp. 7; T, spp. 4), *Phalaenopsis* Blume (Y, spp. 3; T, spp. 2), *Pholidota* Lindl. (Y, spp. 11; T, sp. 1), *Phreatia* Lindl. (Y, sp. 1; T, spp. 4), *Platanthera* Rich. (Y, spp. 22; T, spp. 6), *Pleione* D. Don (Y, spp. 15; T, sp. 1), *Podochilus* Blume (Y, sp. 1), *Pogonia* Juss. (Y, spp. 2; T, sp. 1), *Polystachya* Hook. (Y, sp. 1), *Pomatocalpa* Breda, Kuhl & Hasselt (T, sp. 1), *Porpax* Lindl. (Y, sp. 1), *Pteroceras* Hasselt (Y, spp. 2), *Renanthera* Lour. (Y, spp. 2), *Rhynchostylis* Blume (Y, sp. 1), *Risleya* King & Pantl. (Y, sp. 1), *Robiquetia* Gaudich. (Y, sp. 1), *Sarcoglyphis* Garay (Y, spp. 2), *Satyrium* Sw. (Y, spp. 3), *Schoenorchis* Blume (Y, spp. 2; T, sp. 1), *Sedirea* Garay & H. R. Sweet (Y, sp. 1), *Smithorchis* T. Tang & F. T. Wang (Y, sp. 1), *Smitinandia* Holttum (Y, sp. 1), *Spathoglottis* Blume (Y, sp. 1; T, sp. 1), *Spiranthes* Rich. (Y, sp. 1; T, sp. 1), *Staurochilus* Ridl. (Y, spp. 2; T, sp. 1), *Stereosandra* Blume (Y, sp. 1; T, sp. 1), *Sunipia* Lindl. (Y, spp. 7; T, sp. 1), *Taeniophyllum* Blume (Y, spp. 2; T, spp. 2), *Tainia* Blume (Y, spp. 5; T, spp. 3), *Thelasis* Blume (Y, spp. 2; T, sp. 1), *Thrixspermum* Lour. (Y, spp. 2; T, spp. 9), *Thunia* Rchb. f. (Y, sp. 1), *Tipularia* Nutt. (Y, sp. 1; T, sp. 1), *Trichoglottis* Blume (Y, sp. 1; T, sp. 1), *Tropidia* Lindl. (Y, spp. 2; T, spp. 3), *Tsaiorchis* Tang & F. T. Wang (Y, sp. 1), *Tuberolabium* Yamam. (T, sp. 1), *Tulotis* Raf. (Y, sp. 1; T, sp. 1), *Uncifera* Lindl. (Y, sp. 1), *Vanda* Jones ex R. Br. (Y, spp. 8; T, sp. 1), *Vandopsis* Pfitz. (Y, spp. 2), *Vanilla* Mill. (Y, sp. 1; T, sp. 1), *Vexillabium* F. Maek. (T, spp. 2), *Vrydagzynea* Blume (T, sp. 1), *Yoania* Maxim. (T, sp. 1), *Zeuxine* Lindl. (Y, spp. 5; T, spp. 10).
- Orobanchaceae** (Y, gen. 9; T, gen. 7): *Aeginetia* L. (Y, sp. 1; T, sp. 1), *Boschniakia* C. A. Mey. (Y, sp. 1; T, sp. 1), *Christisonia* Gardner (Y, sp. 1; T, sp. 1), *Euphrasia* L. (Y, sp. 1; T, spp. 3), *Gleadovia* Gamble & Prain (Y, sp. 1), *Melampyrum* L. (Y, sp. 1), *Orobanche* L. (Y, spp. 2; T, sp. 1), *Pedicularis* L. (Y, spp. 150; T, spp. 2), *Striga* Lour. (Y, spp. 3; T, spp. 2).
- Oxalidaceae** (Y, gen. 3; T, gen. 2): *Averrhoa* L. (Y, sp. 1), *Biophytum* DC. (Y, spp. 4; T, sp. 1), *Oxalis* L. (Y, spp. 5; T, spp. 2).
- Paeoniaceae** (Y, gen. 1): *Paeonia* L. (Y, spp. 5).
- Palmae** (Y, gen. 17; T, gen. 5): *Areca* L. (Y, spp. 2), *Arenga* Labill. (Y, spp. 4; T, sp. 1), *Calamus* L. (Y, spp. 23; T, spp. 2), *Caryota* L. (Y, spp. 5), *Chuniophoenix* Burret. (Y, spp. 2), *Cocos* L. (Y, sp. 1), *Daemonorops* Blume (Y, sp. 1), *Guihaia* J. Dransf., S. K. Lee & F. N. Wei (Y, sp. 1), *Licuala* Thunb. (Y, sp. 1), *Livistona* R. Br. (Y, spp. 3; T, sp. 1), *Phoenix* L. (Y, spp. 4; T, sp. 1), *Pinanga* Blume (Y, spp. 5; T, sp. 1), *Plectocomia* Mart. (Y, spp. 3), *Rhapis* L. f. (Y, spp. 3), *Salacca* Reinw. (Y, sp. 1), *Trachycarpus* H. Wendl. (Y, spp. 3), *Wallichia* Roxb. (Y, spp. 6).
- Pandaceae** (Y, gen. 1): *Microdesmis* Hook. f. (Y, sp. 1).
- Pandanaceae** (Y, gen. 1; T, gen. 2): *Freycinetia* Gaudich. (T, sp. 1), *Pandanus* Parkinson (Y, spp. 2; T, sp. 1).
- Papaveraceae** (Y, gen. 6; T, gen. 3): *Argemone* L. (Y, sp. 1; T, sp. 1), *Dicranostigma* Hook. f. & Thomson (Y, spp. 2), *Eomecon* Hance (Y, sp. 1), *Macleaya* R. Br. (Y, sp. 1; T, sp. 1), *Meconopsis* R. Vig. (Y, spp. 17), *Papaver* L. (Y, spp. 3; T, spp. 2).
- Passifloraceae** (Y, gen. 2; T, gen. 2): *Adenia* Forssk. (Y, spp. 2; T, sp. 1), *Passiflora* L. (Y, spp. 12; T, spp. 3).
- Pentaphragmataceae** (Y, gen. 1): *Pentaphragma* Wall. (Y, sp. 1).
- Pentaphyllacaceae** (Y, gen. 1): *Pentaphyllax* Gardner & Champ. (Y, sp. 1).
- Philydraceae** (T, gen. 1): *Philydrum* Banks (T, sp. 1).
- Phrymaceae** (Y, gen. 2; T, gen. 1): *Mazus* Lour. (Y, spp. 10; T, spp. 7), *Phryma* L. (Y, sp. 1).
- Pinaceae** (Y, gen. 8; T, gen. 6): *Abies* Mill. (Y, spp. 6; T, sp. 1), *Keteleeria* Carrière (Y, spp. 3; T, sp. 1), *Larix* Mill. (Y, sp. 1), *Picea* A. Dietr. (Y, spp. 2; T, sp. 1), *Pinus* L. (Y, spp. 15; T, spp. 3), *Pseudolarix* Gordon (Y, sp. 1), *Pseudotsuga* Carrière (Y, spp. 2; T, sp. 1), *Tsuga* Carrière (Y, spp. 3; T, sp. 1).
- Piperaceae** (Y, gen. 3; T, gen. 2): *Peperomia* Ruiz & Pav. (Y, spp. 6; T, spp. 6), *Piper* L. (Y, spp. 41; T, spp. 8), *Zippelia* Blume (Y, sp. 1).
- Pittosporaceae** (Y, gen. 1; T, gen. 1): *Pittosporum* Banks (Y, spp. 28; T, spp. 5).
- Plantaginaceae** (Y, gen. 10; T, gen. 7): *Bacopa* Aubl. (Y, sp. 1; T, sp. 1), *Callitriche* L. (Y, spp. 2; T, spp. 3), *Hippuris* L. (Y, sp. 1), *Lagotis* Geartn. (Y, spp. 5), *Limnophila* R. Br. (Y, spp. 8; T, spp. 7), *Linaria* Mill. (Y, spp. 3), *Plantago* L. (Y, spp. 7; T, spp. 5), *Scoparia* L. (Y, sp. 1; T, sp. 1), *Veronica* L. (Y, spp. 19; T, spp. 10), *Veronicastrum* Heister (Y, spp. 5; T, spp. 2).
- Plumbaginaceae** (Y, gen. 2; T, gen. 2): *Ceratostigma* Bunge (Y, spp. 2), *Limonium* Mill. (T, spp. 2), *Plumbago* L. (Y, spp. 3; T, sp. 1).
- Poaceae** (Y, gen. 175; T, gen. 123): *Achnatherum* P. Beauv. (Y, spp. 4), *Acidosasa* C. D. Chu & C. S. Chao (Y, sp. 1), *Acrachne* Wight & Arn. (Y, sp. 1), *Agropogon* P. Fourn. (Y, sp. 1), *Agropyron* Gaertn. (T, spp. 2), *Agrostis* L. (Y, spp. 31; T, spp. 2), *Alloteropsis* J. Presl (Y, sp. 1; T, sp. 1), *Alopecurus* L. (Y, spp. 2; T, sp. 1), *Ampelocalamus* S. L. Chen, T. H. Wen & G. Y. Sheng (Y, spp. 5), *Andropogon* L. (Y, spp. 3), *Anisachne* Keng (Y, sp. 1), *Aniselytron* Merr. (Y, sp. 1; T, spp. 2), *Anthoxanthum* L. (Y, spp. 3; T, sp. 1), *Apluda* L. (Y, sp. 1; T, sp. 1), *Apocopis* Nees (Y, spp. 4),

Aristida L. (Y, spp. 5; T, sp. 1), *Arthraxon* P. Beauv. (Y, spp. 13; T, spp. 3), *Arundinaria* Michx. (Y, spp. 5; T, spp. 6), *Arundinella* Raddi (Y, spp. 16; T, spp. 3), *Arundo* L. (Y, sp. 1; T, spp. 2), *Avena* L. (Y, spp. 5; T, spp. 2), *Axonopus* P. Beauv. (Y, sp. 1; T, spp. 2), *Bambusa* Schreb. (Y, spp. 21; T, spp. 18), *Beckmannia* Host (Y, sp. 1), *Bonia* Balansa (Y, sp. 1), *Bothriochloa* Kuntze (Y, spp. 9; T, spp. 3), *Brachiaria* Griseb. (Y, spp. 7; T, spp. 4), *Brachyelytrum* P. Beauv. (Y, sp. 1), *Brachypodium* P. Beauv. (Y, spp. 3; T, spp. 2), *Briza* L. (Y, sp. 1; T, sp. 1), *Bromus* L. (Y, spp. 15; T, spp. 4), *Calamagrostis* Adans. (Y, spp. 3; T, sp. 1), *Capillipedium* Stapf (Y, spp. 2; T, spp. 3), *Catabrosa* P. Beauv. (Y, sp. 1), *Cenchrus* L. (Y, spp. 2; T, sp. 1), *Centotheca* Desv. (Y, sp. 1; T, sp. 1), *Cephalostachyum* Munro (Y, spp. 6), *Chimonobambusa* Makino (Y, spp. 9; T, sp. 1), *Chimonocalamus* J. R. Kue (Y, spp. 9), *Chloris* Sw. (Y, spp. 3; T, spp. 4), *Chrysopogon* Trin. (Y, spp. 2; T, sp. 1), *Coelachne* R. Br. (Y, sp. 1), *Coelorachis* Brongn. (Y, spp. 2), *Coix* L. (Y, spp. 6; T, sp. 1), *Crypsis* Aiton. (Y, sp. 1), *Cymbopogon* Spreng. (Y, spp. 19; T, sp. 1), *Cynodon* Rich. (Y, sp. 1; T, spp. 2), *Cyrtococcum* Stapf (Y, spp. 4; T, spp. 2), *Dactylis* L. (Y, sp. 1; T, sp. 1), *Dactyloctenium* Willd. (Y, sp. 1; T, sp. 1), *Danthonia* DC. (Y, sp. 1), *Dendrocalamus* Nees (Y, spp. 22; T, spp. 5), *Deschampsia* P. Beauv. (Y, spp. 3; T, sp. 1), *Deyeuxia* Clarion (Y, spp. 16; T, spp. 2), *Dichanthium* Willemet (Y, spp. 4; T, spp. 2), *Digitaria* Haller (Y, spp. 20; T, spp. 13), *Dimeria* R. Br. (Y, spp. 2; T, spp. 2), *Dinebra* Jacq. (Y, sp. 1), *Diplachne* P. Beauv. (Y, sp. 1; T, sp. 1), *Drepanostachyum* Keng f. (Y, spp. 2), *Duthiea* Hack. (Y, sp. 1), *Eccoilopus* Steud. (T, spp. 2), *Echinochloa* P. Beauv. (Y, spp. 9; T, spp. 3), *Eleusine* Gaertn. (Y, spp. 2; T, spp. 2), *Elymus* L. (Y, spp. 6), *Elytrigia* Desv. (Y, sp. 1), *Elytrophorus* P. Beauv. (Y, sp. 1), *Enneapogon* Desv. (Y, sp. 1), *Enteropogon* Nees (Y, sp. 1; T, spp. 2), *Eragrostiella* Bor (Y, sp. 1), *Eragrostis* Wolf (Y, spp. 23; T, spp. 17), *Eremochloa* Buese (Y, spp. 3; T, spp. 2), *Erianthus* Michx. (Y, spp. 4; T, spp. 2), *Eriochloa* Kunth (Y, sp. 1; T, spp. 2), *Eulalia* Kunth (Y, spp. 12; T, spp. 3), *Eulaliopsis* Honda (Y, sp. 1; T, sp. 1), *Eustachys* Desv. (T, sp. 1), *Fargesia* Franch. (Y, spp. 39), *Ferocalamus* J. R. Xue & Keng f. (Y, spp. 2), *Festuca* L. (Y, spp. 27; T, spp. 7), *Gaoligongshania* D. Z. Li, Hsueh & N. H. Xia (Y, sp. 1), *Garnotia* Brongn. (Y, spp. 3; T, sp. 1), *Germainia* Balansa & Poitr. (Y, sp. 1), *Gigantochloa* Kurz (Y, spp. 6; T, sp. 1), *Glyceria* R. Br. (Y, spp. 4; T, sp. 1), *Hackelochloa* Kuntze (Y, spp. 2; T, sp. 1), *Harpachne* Hochst. (Y, sp. 1), *Helictotrichon* Besser (Y, spp. 6; T, sp. 1), *Hemarthria* R. Br. (Y, spp. 4; T, sp. 1), *Heteropogon* Pers. (Y, spp. 3; T, sp. 1), *Hierochloe* R. Br. (Y, sp. 1), *Hordeum* L. (Y, spp. 2; T, sp. 1), *Hygroryza* Nees (Y, sp. 1; T, sp. 1), *Hymenachne* P. Beauv. (Y, spp. 3; T, sp. 1), *Hyparrhenia* Andersson (Y, spp. 5), *Hystrix* Moench (Y, sp. 1), *Ichnanthus* P. Beauv. (Y, sp. 1; T, sp. 1), *Imperata* Cirillo (Y, sp. 1), *Indocalamus* Nakai (Y, sp. 1), *Indosasa* McClure (Y, spp. 5), *Isachne* R. Br. (Y, spp. 9; T, spp. 8, T), *Ischaemum* L. (Y, spp. 6; T, spp. 7), *Koeleria* Pers. (Y, sp. 1), *Leersia* Sw. (Y, sp. 1; T, sp. 1), *Leptaspis* R. Br. (T, sp. 1), *Leptocanna* L. C. Chia & H. L. Fung (Y, sp. 1), *Leptochloa* P. Beauv. (Y, spp. 2; T, spp. 2), *Lepturus* R. Br. (T, sp. 1), *Littledalea* Hemsl. (Y, spp. 2), *Lolium* L. (Y, spp. 2; T, spp. 2), *Lophatherum* Brongn. (Y, sp. 1; T, sp. 1), *Melica* L. (Y, spp. 4; T, sp. 1), *Melocalamus* Benth. (Y, spp. 3), *Microchloa* R. Br. (Y, sp. 1), *Microstegium* Nees (Y, spp. 8; T, spp. 8), *Milium* L. (Y, sp. 1; T, sp. 1), *Miscanthus* Andersson (Y, spp. 8; T, spp. 2), *Muhlenbergia* Schreb. (Y, spp. 5; T, sp. 1), *Narenga* Bor (T, sp. 1), *Neohusnotia* A. Camus (Y, sp. 1), *Neyraudia* Hook. f. (Y, sp. 1; T, sp. 1), *Ophiuros* C. F. Gaertn. (Y, sp.

1), *Oplismenus* P. Beauv. (Y, spp. 4; T, spp. 3), *Orthoraphium* Nees (Y, sp. 1), *Oryza* L. (Y, spp. 4; T, spp. 2), *Oryzopsis* Michx. (Y, spp. 6; T, sp. 1), *Ottochloa* Dandy (Y, sp. 1; T, sp. 1), *Panicum* L. (Y, spp. 14; T, spp. 12), *Paspalidium* Stapf (Y, spp. 2; T, spp. 2), *Paspalum* L. (Y, spp. 10; T, spp. 13), *Pennisetum* Rich. (Y, spp. 9; T, spp. 4), *Perotis* Aiton (Y, spp. 2; T, spp. 2), *Phacelurus* Griseb. (Y, sp. 1), *Phaenosperma* Munro (Y, sp. 1; T, sp. 1), *Phalaris* L. (Y, spp. 4; T, spp. 2), *Phleum* L. (Y, spp. 2; T, sp. 1), *Phragmites* Adans. (Y, spp. 3; T, spp. 2), *Phyllostachys* Siebold & Zucc. (Y, spp. 12; T, spp. 8), *Poa* L. (Y, spp. 78; T, spp. 7), *Pogonatherum* P. Beauv. (Y, spp. 2; T, spp. 2), *Polypogon* Desf. (Y, spp. 2; T, spp. 2), *Polytoca* R. Br. (Y, sp. 1), *Pseudechinolaena* Stapf (Y, sp. 1), *Pseudopogonatherum* A. Camus (Y, spp. 2), *Pseudoraphis* Griff. (Y, sp. 1; T, sp. 1), *Pseudosasa* Makino (T, spp. 2), *Pseudosorghum* A. Camus (Y, spp. 2), *Pseudostachyum* Munro (Y, sp. 1), *Ptilagrostis* Griseb. (Y, spp. 3), *Qiongzhusia* (Wen & Ohmberger) Hsueh & Yi (Y, spp. 2), *Racemobambos* Holttum (Y, sp. 1), *Rhytachne* Desv. (Y, spp. 2), *Roegneria* K. Koch (Y, spp. 20), *Rottboellia* L. f. (Y, sp. 1; T, sp. 1), *Saccharum* L. (Y, spp. 7; T, spp. 4), *Sacciolepis* Nash (Y, spp. 3; T, sp. 1), *Schizachne* Hack. (Y, sp. 1), *Schizachyrium* Nees (Y, spp. 3; T, sp. 1), *Schizostachyum* Thomas Nees (Y, spp. 3; T, spp. 2), *Sehima* Forssk. (Y, sp. 1), *Semiarundinaria* Nakai (T, sp. 1), *Setaria* P. Beauv. (Y, spp. 13; T, spp. 9), *Shibataea* Makino (T, sp. 1), *Sinobambusa* Makino (Y, spp. 2; T, spp. 2), *Sorghum* Moench (Y, spp. 7; T, spp. 5), *Sphaerocaryum* Nees (Y, sp. 1; T, sp. 1), *Spinifex* L. (T, sp. 1), *Spodiopogon* Trin. (Y, spp. 4; T, sp. 1), *Sporobolus* R. Br. (Y, spp. 4; T, spp. 2), *Stenotaphrum* Trin. (Y, sp. 1), *Stipa* L. (Y, spp. 3), *Stipagrostis* Nees (Y, sp. 1), *Thaumastochloa* C. E. Hubb. (T, spp. 2), *Themeda* Forssk. (Y, spp. 14; T, spp. 2), *Thuarea* Pers. (T, sp. 1), *Thyrsia* Stapf (Y, sp. 1), *Thyrsostachys* Gamble (Y, spp. 2; T, sp. 1), *Thysanolaena* Nees (Y, sp. 1; T, sp. 1), *Tragus* Haller (Y, spp. 2), *Trikeria* Bor (Y, sp. 1), *Tripogon* Roem. & Schult. (Y, spp. 7; T, sp. 1), *Trisetum* Pers. (Y, spp. 5; T, sp. 1), *Triticum* L. (Y, sp. 1; T, sp. 1), *Urochloa* P. Beauv. (Y, spp. 5), *Vulpia* C. C. Gmel. (T, sp. 1), *Yushania* Keng f. (Y, spp. 27; T, sp. 1), *Zizania* L. (Y, sp. 1; T, sp. 1), *Zoysia* Willd. (Y, spp. 3; T, spp. 4).

Podocarpaceae (Y, gen. 1; T, gen. 2): *Nageia* Gaertn. (T, spp. 2), *Podocarpus* L'Hér. (Y, spp. 8; T, spp. 4).

Podostemaceae (Y, gen. 1), *Hydrobryum* Endl. (Y, sp. 1).

Polemoniaceae (Y, gen. 1): *Polemonium* L. (Y, sp. 1).

Polygalaceae (Y, gen. 4; T, gen. 3): *Epirixanthes* Blume (T, sp. 1), *Polygala* L. (Y, spp. 24; T, spp. 5), *Salomonina* Lour. (Y, spp. 3; T, sp. 1), *Securidaca* L. (Y, spp. 2), *Xanthophyllum* Roxb. (Y, spp. 3).

Polygonaceae (Y, gen. 9; T, gen. 3): *Antenorion* Raf. (Y, sp. 1), *Fagopyrum* Mill. Y. (Y, spp. 10; T, sp. 1), *Fallopia* Adans. (Y, spp. 6), *Koenigia* L. (Y, sp. 1), *Oxyria* Hill (Y, spp. 2), *Polygonum* L. (Y, spp. 64; T, spp. 35), *Reynoutria* Houtt. (Y, sp. 1), *Rheum* L. (Y, spp. 12), *Rumex* L. (Y, spp. 11; T, spp. 6).

Pontederiaceae (Y, gen. 2; T, gen. 2): *Eichhornia* Kunth (Y, sp. 1; T, sp. 1), *Monochoria* C. Presl (Y, spp. 2; T, sp. 1).

Portulacaceae (Y, gen. 2; T, gen. 2): *Portulaca* L. (Y, spp. 4; T, spp. 3), *Talinum* Adans. (Y, sp. 1; T, sp. 1).

Potamogetonaceae (Y, gen. 1; T, gen. 1): *Potamogeton* L. (Y, spp. 12; T, spp. 9).

Primulaceae (Y, gen. 4; T, gen. 5): *Anagallis* L. (T, sp. 1), *Androsace* L. (Y, spp. 23; T, sp. 1), *Lysimachia* L. (Y, spp. 65; T, spp. 10), *Omphalogramma* Franch. (Y, spp. 6),

- Primula* L. (Y, spp. 127; T, sp. 1), *Stimpsonia* C. Wright (T, sp. 1).
- Proteaceae** (Y, gen. 2; T, gen. 1): *Helicia* Lour. (Y spp. 12; T, spp. 3), *Heliciopsis* Sleum. (Y, sp. 1).
- Rafflesiaceae** (Y, gen. 1): *Sapria* Griff. (Y, sp. 1).
- Ranunculaceae** (Y, gen. 28; T, gen. 10): *Aconitum* L. (Y, spp. 66; T, sp. 1), *Actaea* L. (Y, sp. 1), *Adonis* L. (Y, sp. 1), *Anemoclema* (Franch.) W. T. Wang (Y, sp. 1), *Anemone* L. (Y, spp. 25; T, spp. 2), *Aquilegia* L. (Y, sp. 1), *Asteropyrum* J. R. Drumm. & Hutch. (Y, spp. 2), *Batrachium* (DC.) S. F. Gray (Y, spp. 3), *Beesia* Balf. f. & W. W. Sm. (Y, sp. 1), *Calathodes* Hook. f. & Thomson (Y, spp. 2; T, sp. 1), *Callianthemum* C. A. Mey. (Y, sp. 1), *Caltha* L. (Y, spp. 3), *Cimicifuga* Wernisch. (Y, spp. 4; T, sp. 1), *Clematis* L. (Y, spp. 56; T, spp. 15), *Coptis* Salisb. (Y, spp. 3; T, sp. 1), *Delphinium* L. (Y, spp. 49), *Dichocarpum* W. T. Wang & P. K. Hsiao (Y, spp. 5; T, sp. 1), *Halerpestes* Greene (Y, sp. 1), *Kingdonia* Balf. f. & W. W. Sm. (Y, sp. 1), *Metanemone* W. T. Wang (Y, sp. 1), *Naravelia* Adans. (Y, sp. 1), *Oxygraphis* Bunge (Y, spp. 3), *Paraquilegia* J. R. Drumm. & Hutch. (Y, sp. 1), *Pulsatilla* Mill. (Y, sp. 1), *Ranunculus* L. (Y, spp. 35; T, sp. 11), *Souliea* Franch. (Y, sp. 1), *Thalictrum* L. (Y, spp. 35; T, spp. 4), *Trollius* L. (Y, spp. 6; T, sp. 1).
- Rhamnaceae** (Y, gen. 14; T, gen. 6): *Alphitonia* Reissek (Y, sp. 1), *Berchemia* Neck. (Y, spp. 13; T, spp. 4), *Berchemiella* Nakai (Y, sp. 1), *Chaydaia* Pit. (Y, sp. 1), *Colubrina* Rich. (Y, sp. 1; T, sp. 1), *Gouania* Jacq. (Y, spp. 2), *Hovenia* Thunb. (Y, sp. 1), *Paliurus* Mill. (Y, spp. 3; T, sp. 1), *Rhamnella* Miq. (Y, spp. 4), *Rhamnus* L. (Y, spp. 30; T, spp. 7), *Sageretia* Brongn. (Y, spp. 20; T, spp. 2), *Scutia* Comm. (Y, sp. 1), *Ventilago* Gaertn. (Y, spp. 5; T, spp. 2), *Ziziphus* Mill. (Y, spp. 10).
- Rhizophoraceae** (Y, gen. 2; T, gen. 2): *Carallia* Roxb. (Y, spp. 2), *Kandelia* (DC.) Wight & Arn. (T, sp. 1), *Pellacalyx* Korth. (Y, sp. 1), *Rhizophora* L. (T, sp. 1).
- Rosaceae** (Y, gen. 41; T, gen. 23): *Agrimonia* L. (Y, sp. 1; T, sp. 1), *Amygdalus* L. (Y, spp. 4), *Aria* (Pers.) Host (T, sp. 1), *Armeniaca* Scop. (Y, spp. 2), *Aruncus* L. (Y, spp. 2), *Cerasus* Mill. (Y, spp. 20), *Chaenomeles* Lindl. (Y, spp. 4), *Coluria* R. Br. (Y, spp. 2), *Cotoneaster* Medik. (Y, spp. 40; T, spp. 5), *Crataegus* L. (Y, spp. 7), *Cydonia* Mill. (Y, sp. 1), *Dichotomanthes* Kurz (Y, sp. 1), *Docynia* Decne. (Y, spp. 2), *Duchesnea* Sm. (Y, spp. 2; T, spp. 2), *Eriobotrya* Lindl. (Y, spp. 12; T, spp. 2), *Filipendula* Mill. (Y, sp. 1; T, sp. 1), *Fragaria* L. (Y, spp. 7; T, sp. 1), *Geum* L. (Y, spp. 2), *Kerria* DC. (Y, sp. 1), *Laurocerasus* Duham. (Y, spp. 9), *Malus* Mill. (Y, spp. 12; T, spp. 2), *Neillia* D. Don (Y, spp. 8), *Osteomeles* Lindl. (Y, sp. 1; T, sp. 1), *Padus* Mill. (Y, spp. 7), *Photinia* Lindl. (Y, spp. 15; T, spp. 2), *Potentilla* L. (Y, spp. 40; T, spp. 6), *Pourthiaea* Decne. (T, sp. 1), *Prinsepia* Royle (Y, sp. 1; T, sp. 1), *Prunus* L. (Y, spp. 2; T, spp. 12), *Pygeum* Gaertn. (Y, spp. 5), *Pyracantha* M. Roem. (Y, spp. 4; T, sp. 1), *Pyrus* L. (Y, spp. 7; T, spp. 2), *Raphiolepis* Lindl. (Y, spp. 2; T, sp. 1), *Rosa* L. (Y, spp. 41; T, spp. 8), *Rubus* L. (Y, spp. 104; T, spp. 34), *Sanguisorba* L. (Y, spp. 2), *Sibbaldia* L. (Y, spp. 8; T, sp. 1), *Sibiraea* Maxim. (Y, sp. 1), *Sorbaria* (Ser.) A. Braun (Y, sp. 1), *Sorbus* L. (Y, spp. 48; T, sp. 1), *Spenceria* Trimen (Y, sp. 1), *Spiraea* L. (Y, spp. 26; T, spp. 4), *Stephanandra* Sieb. & Zucc. (T, sp. 1), *Stranvaesia* Lindl. (Y, spp. 4).
- Rubiaceae** (Y, gen. 68; T, gen. 39): *Acranthera* Arn. (Y, sp. 1), *Adina* Salisb. (Y, spp. 2), *Aidia* Lour. (Y, spp. 5), *Argostemma* Wall. (Y, spp. 3; T, sp. 1), *Borreria* G. Mey. (Y, spp. 3), *Brachytome* Hook. f. (Y, spp. 3), *Caelospermum* Blume (Y, sp. 1), *Canthium* Lam. (Y, spp. 3; T, sp. 1), *Catunaregam* Wolf (Y, sp. 1), *Cephaelis* Sw. (Y, sp. 1), *Cephalanthus* L. (Y, sp. 1; T, sp. 1), *Chassalia* Comm. (Y, sp. 1), *Clarkella* Hook. f. (Y, sp. 1), *Coptosapelta* Korth. (Y, sp. 1; T, sp. 1), *Damnacanthus* Gaertn. f. (Y, spp. 6; T, spp. 2), *Dentella* J. R. Forst. & G. Forst. (Y, sp. 1; T, sp. 1), *Diodia* L. (T, sp. 1), *Diplospora* DC. (Y, spp. 3), *Duperrea* Pierre ex Pit. (Y, sp. 1), *Emmenopterys* Oliv. (Y, sp. 1), *Fagerlindia* Tirveng. (Y, sp. 1), *Galium* L. (Y, spp. 17; T, spp. 10), *Gardenia* J. Ellis (Y, spp. 2; T, sp. 1), *Geophila* D. Don (Y, sp. 1; T, sp. 1), *Guettarda* L. (T, sp. 1), *Hayataella* Masam. (T, sp. 1), *Hedyotis* L. (Y, spp. 21; T, spp. 9), *Himalrandia* T. Yamaz. (Y, sp. 1), *Hymenodictyon* Wall. (Y, spp. 2), *Hyptianthera* Wight & Arn. (Y, sp. 1), *Ixora* L. (Y, spp. 16; T, sp. 1), *Kelloggia* Torr. (Y, sp. 1), *Knoxia* L. (Y, spp. 2; T, sp. 1), *Lasianthus* Jack (Y, spp. 21; T, sp. 14), *Leptodermis* Wall. (Y, spp. 16), *Leptomischus* Drake (Y, spp. 4), *Lerchea* L. (Y, spp. 2), *Litosanthes* Blume (Y, sp. 1; T, sp. 1), *Luculia* Sweet (Y, spp. 3), *Metadina* Bakh. f. (Y, sp. 1), *Mitchella* L. (T, sp. 1), *Mitragyna* Korth. (Y, sp. 1), *Morinda* L. (Y, spp. 15; T, spp. 3), *Mussaenda* L. (Y, spp. 21; T, spp. 2), *Mycetia* Reinw. (Y, spp. 11), *Myrioneuron* R. Br. (Y, spp. 4), *Nauclea* L. (Y, sp. 1), *Neanotis* W. H. Lewis (Y, spp. 4; T, sp. 1), *Neohymenopogon* Bennet (Y, spp. 2), *Neolamarckia* J. Bosser (Y, sp. 1), *Neonauclea* Merr. (Y, spp. 3; T, sp. 1), *Nertera* Banks (Y, spp. 2; T, spp. 2), *Ophiorrhiza* L. (Y, spp. 42; T, spp. 4), *Oxyceros* Lour. (Y, spp. 3), *Paederia* L. (Y, spp. 7; T, spp. 2), *Pavetta* L. (Y, spp. 5; T, sp. 1), *Porterandia* Ridl. (Y, sp. 1), *Prismatomeris* Thwaites. (Y, sp. 1), *Psychotria* L. (Y, spp. 13; T, spp. 4), *Randia* L. (T, spp. 5), *Richardia* L. (T, spp. 2), *Rubia* L. (Y, spp. 19; T, spp. 3), *Saprosma* Blume (Y, spp. 3), *Schizomussaenda* H. L. Li (Y, sp. 1), *Serissa* Comm. (Y, spp. 2; T, sp. 1), *Sinoadina* Ridsdale (Y, sp. 1; T, sp. 1), *Spermacece* L. (T, spp. 5), *Spiradictis* Blume (Y, spp. 6), *Tarenna* Gaertn. (Y, spp. 7; T, spp. 3), *Tarennoidea* Tirveng. & Sastre (Y, sp. 1), *Theligonum* L. (T, sp. 1), *Timonius* DC. (T, sp. 1), *Trailliaedoxa* W. W. Sm. & Forrest (Y, sp. 1), *Tricalysia* A. Rich. (T, sp. 1), *Uncaria* Schreb. (Y, spp. 9; T, spp. 2), *Urophyllum* Wall. (Y, spp. 3), *Wendlandia* Bartl. (Y, spp. 22; T, spp. 3), *Xanthophytum* Reinw. (Y, sp. 1).
- Ruppiaceae** (T, gen. 1): *Ruppia* L. (T, sp. 1).
- Rutaceae** (Y, gen. 20; T, gen. 13): *Acronychia* J. R. Forst & G. Forst. (Y, sp. 1; T, sp. 1), *Aegle* Corrêa (Y, sp. 1), *Atalantia* Corrêa (Y, spp. 6), *Boenninghausenia* Rechb. (Y, spp. 2; T, sp. 1), *Citrus* L. (Y, spp. 13; T, spp. 4), *Clausena* Burm. f. (Y, spp. 11; T, spp. 2), *Euodia* J. R. (Y, spp. 11), *Evodia* Lam. (Y, sp. 1), *Fortunella* Swingle (Y, spp. 3), *Glycosmis* Corrêa (Y, spp. 8; T, sp. 1), *Luvunga* Buch.-Ham. (Y, spp. 2), *Melicope* J. R. Forst. & G. Forst. (T, spp. 3), *Micromelum* Blume (Y, spp. 3), *Murraya* J. König (Y, spp. 4; T, spp. 3), *Orixa* Thunb. (Y, sp. 1), *Paramignya* Wight (Y, spp. 2), *Phellodendron* Rupr. (Y, sp. 1; T, sp. 1), *Poncirus* Raf. (Y, spp. 2), *Severinia* Ten. (T, sp. 1), *Skimmia* Thunb. (Y, sp. 1; T, spp. 2), *Tetradium* Lour. (T, spp. 2), *Toddalia* Juss. (Y, sp. 1; T, sp. 1), *Zanthoxylum* L. (Y, spp. 28; T, spp. 9).
- Sabiaceae** (Y, gen. 2; T, gen. 2): *Meliosma* Blume (Y, spp. 22; T, spp. 4), *Sabia* Colebr. (Y, spp. 13; T, spp. 2).
- Salicaceae** (Y, gen. 4; T, gen. 3): *Casearia* Jacq. (Y, spp. 7; T, sp. 1), *Homalium* Jacq. (Y, sp. 1; T, sp. 1), *Populus* L. (Y, spp. 16), *Salix* L. (Y, spp. 87; T, spp. 5).
- Santalaceae** (Y, gen. 6; T, gen. 1): *Dendrotrophe* Miq. (Y, spp. 7), *Osyris* L. (Y, sp. 1), *Phacellaria* Benth. (Y, spp. 5), *Pyrularia* Michx. (Y, sp. 1), *Scleropyrum* Arn. (Y, sp. 1), *Thesium* L. (Y, spp. 9; T, sp. 1).
- Sapindaceae** (Y, gen. 20; T, gen. 9): *Acer* L. (Y, spp. 51; T, spp. 4), *Allophylus* L. (Y, spp. 3; T, sp. 1), *Amesiodendron* Hu (Y, sp. 1), *Arytera* Blume (Y, sp. 1), *Cardiospermum* L.

- (Y, sp. 1; T, sp. 1), *Delavaya* Franch. (Y, sp. 1), *Dimocarpus* Lour. (Y, spp. 3), *Dipteronia* Oliv. (Y, sp. 1), *Dodonaea* Mill. (Y, sp. 1; T, sp. 1), *Eurycorymbus* Hand.-Mazz. (Y, sp. 1; T, sp. 1), *Harpullia* Roxb. (Y, sp. 1), *Koelreuteria* Laxm. (Y, spp. 2; T, sp. 1), *Lepisanthes* Blume (Y, spp. 3), *Litchi* Sonn. (Y, sp. 1; T, sp. 1), *Mischocarpus* Blume (Y, spp. 2), *Nephelium* L. (Y, sp. 1), *Pavieasia* Pierre (Y, sp. 1), *Pometia* J. R. Forst. & G. Forst. (Y, sp. 1; T, sp. 1), *Sapindus* L. (Y, spp. 4; T, sp. 1), *Xerospermum* Blume (Y, sp. 1).
- Sapotaceae** (Y, gen. 7; T, gen. 2): *Eberhardtia* Lecomte (Y, spp. 2), *Madhuca* J. F. Gmel. (Y, sp. 1), *Palaquium* Blanco (T, sp. 1), *Planchonella* Pierre (Y, spp. 2; T, spp. 2), *Pouteria* Aubl. (Y, sp. 1), *Sarcosperma* Hook. f. (Y, spp. 3), *Sinosideroxylon* (Engl.) Aubr. (Y, sp. 1), *Xantolis* Raf. (Y, spp. 3).
- Sargentodoxaceae** (Y, gen. 1): *Sargentodoxa* Rehder & E. H. Wilson (Y, sp. 1).
- Saururaceae** (Y, gen. 3; T, gen. 2): *Gymnotheca* Decne. (Y, sp. 1), *Houttuynia* Thunb. (Y, sp. 1; T, sp. 1), *Saururus* L. (Y, sp. 1; T, sp. 1).
- Saxifragaceae** (Y, gen. 9; T, gen. 7): *Astilbe* Buch.-Ham. (Y, spp. 3; T, spp. 2), *Bergenia* Moench (Y, spp. 2), *Cardiandra* Sieb. & Zucc. (T, sp. 1), *Chrysosplenium* L. (Y, spp. 11; T, spp. 2), *Mitella* L. (T, sp. 1), *Parnassia* L. (Y, spp. 20; T, sp. 1), *Penthorum* L. (Y, sp. 1), *Rodgersia* A. Gray (Y, spp. 3), *Saniculiphyllum* C. Y. Wu & Ku (Y, sp. 1), *Saxifraga* L. (Y, spp. 103; T, sp. 1), *Tiarella* L. (Y, sp. 1; T, sp. 1).
- Schisandraceae** (Y, gen. 3; T, gen. 3): *Illicium* L. (Y, spp. 12; T, spp. 3), *Kadsura* Juss. (Y, spp. 7; T, spp. 2), *Schisandra* Michx. (Y, spp. 11; T, sp. 1).
- Schoepfiaceae** (Y, gen. 1; T, gen. 1): *Schoepfia* Schreb. (Y, spp. 2; T, sp. 1).
- Scrophulariaceae** (Y, gen. 29; T, gen. 12): *Adenosma* R. Br. (Y, spp. 3), *Alectra* Thunb. (Y, sp. 1; T, sp. 1), *Brandisia* Hook. f. & Thomson (Y, spp. 6), *Buchnera* L. (Y, sp. 1), *Centranthera* R. Br. (Y, spp. 2; T, sp. 1), *Cyrtandromoea* Zoll. (Y, spp. 2), *Deinostema* T. Yamaz. (T, spp. 2), *Dopatrium* Buch.-Ham. (Y, sp. 1; T, sp. 1), *Ellisiophyllum* Maxim. (Y, sp. 1; T, sp. 1), *Gratiola* L. (Y, spp. 2), *Hemiphragma* Wall. (Y, sp. 1; T, sp. 1), *Lancea* Hook. f. & Thomson (Y, spp. 2), *Legazpia* Blanco (T, sp. 1), *Limosella* L. (Y, sp. 1), *Lindenbergia* Lehm. (Y, spp. 4), *Microcarpaea* R. Br. (Y, sp. 1; T, sp. 1), *Mimulicalyx* P. C. Tsoong (Y, spp. 2), *Mimulus* L. (Y, spp. 3), *Myoporum* Banks & Sol. (T, sp. 1), *Neopicrorhiza* D. Y. Hong (Y, sp. 1), *Petitmenginina* Bonati (Y, sp. 1), *Phtheirospermum* Bunge (Y, spp. 3; T, sp. 1), *Picria* Lour. (Y, sp. 1), *Pseudolysimachion* (W. D. J. Koch) Opiz (Y, sp. 1), *Pterygiella* Oliv. (Y, spp. 4), *Rehmannia* Libosch. (Y, sp. 1), *Scrophularia* L. (Y, spp. 11; T, sp. 1), *Siphonostegia* Benth (Y, sp. 1; T, sp. 1), *Sopubia* Buch.-Ham. (Y, sp. 1), *Verbascum* L. (Y, spp. 2), *Wightia* Wall. (Y, spp. 2), *Xizangia* D. Y. Hong (Y, sp. 1).
- Simaroubaceae** (Y, gen. 3; T, gen. 3): *Ailanthus* Desf. (Y, spp. 5; T, sp. 2), *Brucea* J. F. Mill. (Y, spp. 2; T, sp. 1), *Picrasma* Blume (Y, spp. 2; T, sp. 1).
- Sladeniaceae** (Y, gen. 1): *Sladenia* Kurz (Y, sp. 1).
- Smilacaceae** (Y, gen. 2; T, gen. 2): *Heterosmilax* Kunth (Y, spp. 8; T, spp. 3), *Smilax* L. (Y, spp. 47; T, spp. 18).
- Solanaceae** (Y, gen. 11; T, gen. 5): *Anisodus* Link (Y, spp. 4), *Atropanthe* Pascher (Y, sp. 1), *Hyoscyamus* L. (Y, sp. 1), *Lycianthes* (Dunal) Hassl. (Y, spp. 6; T, spp. 2), *Lycium* L. (Y, spp. 2), *Mandragora* L. (Y, sp. 1), *Physaliastrum* Makino (Y, spp. 2; T, sp. 1), *Physalis* L. (Y, spp. 4; T, spp. 2), *Scopolia* Jacq. (Y, sp. 1), *Solanum* L. (Y, spp. 29; T, spp. 19), *Tubocapsicum* (Wettst.) Makino (Y, sp. 1; T, sp. 1).
- Sonneratiaceae** (Y, gen. 1): *Duabanga* Buch.-Ham. (Y, sp. 1).
- Sphenocleaceae** (Y, gen. 1; T, gen. 1): *Sphenoclea* Gaertn. (Y, sp. 1; T, sp. 1).
- Stachyuraceae** (Y, gen. 1; T, gen. 1): *Stachyurus* Sieb. & Zucc. (Y, spp. 8; T, sp. 1).
- Staphyleaceae** (Y, gen. 4; T, gen. 2): *Euscaphis* Sieb. & Zucc. (Y, sp. 1; T, sp. 1), *Staphylea* L. (Y, spp. 2), *Tapiscia* Oliv. (Y, sp. 1), *Turpinia* Vent. (Y, spp. 8; T, spp. 3).
- Stemonaceae** (Y, gen. 1; T, gen. 1): *Stemona* Lour. (Y, spp. 2; T, sp. 1).
- Sterculiaceae** (Y, gen. 16; T, gen. 9): *Ambroma* L. f. (Y, sp. 1), *Byttneria* Loebl. (Y, spp. 3), *Commersonia* J. R. Forst. & G. Forst. (Y, sp. 1), *Craigia* W. W. Sm. & W. E. Evans (Y, sp. 1), *Eriolaena* DC. (Y, spp. 5), *Firmiana* Marsili (Y, spp. 3; T, sp. 1), *Helicteres* L. (Y, spp. 8; T, sp. 1), *Heritiera* Aiton (Y, sp. 1; T, sp. 1), *Kleinhovia* L. (T, sp. 1), *Melhania* Forssk. (Y, sp. 1), *Melochia* L. (Y, sp. 1; T, sp. 1), *Paradombeya* Stapf (Y, sp. 1), *Pentapetes* L. (Y, sp. 1), *Pterospermum* Schreb. (Y, spp. 7; T, sp. 1), *Reevesia* Lindl. (Y, spp. 4; T, sp. 1), *Sterculia* L. (Y, spp. 18; T, sp. 1), *Waltheria* L. (Y, sp. 1; T, sp. 1).
- Stylidiaceae** (Y, gen. 1): *Stylidium* Sw. (Y, sp. 1).
- Styracaceae** (Y, gen. 8; T, gen. 2): *Alniphyllum* Matsum. (Y, spp. 2; T, sp. 1), *Bruinsmia* Boerl. & Koord. (Y, sp. 1), *Huodendron* Rehd. (Y, spp. 3), *Melliodendron* Hand.-Mazz. (Y, sp. 1), *Parastyrax* W. W. Sm. (Y, spp. 2), *Pterostyrax* Siebold & Zucc. (Y, spp. 2), *Rehderodendron* Hu (Y, spp. 7), *Styrax* L. (Y, spp. 18; T, spp. 3).
- Symplocaceae** (Y, gen. 1; T, gen. 1): *Symplocos* Jacq. (Y, spp. 41; T, spp. 26).
- Taccaceae** (Y, gen. 1; T, gen. 1): *Tacca* J. R. Forst. & G. Forst. (Y, spp. 2; T, sp. 1).
- Tamaricaceae** (Y, gen. 2): *Myricaria* Desv. (Y, spp. 3), *Tamarix* L. (Y, sp. 1).
- Taxaceae** (Y, gen. 3; T, gen. 2): *Amentotaxus* Pilg. (Y, sp. 1; T, sp. 1), *Taxus* L. (Y, spp. 2; T, sp. 1), *Torreya* Arn. (Y, spp. 2).
- Taxodiaceae** (Y, gen. 5; T, gen. 2): *Cryptomeria* D. Don (Y, sp. 1), *Cunninghamia* R. Br. (Y, sp. 1; T, sp. 1), *Glyptostrobus* Endl. (Y, sp. 1), *Metasequoia* Hu & W. C. Cheng (Y, sp. 1), *Taiwania* Hayata (Y, sp. 1; T, sp. 1).
- Tetracentraceae** (Y, gen. 1): *Tetracentron* Oliv. (Y, sp. 1).
- Tetramelaceae** (Y, gen. 1): *Tetrameles* R. Br. (Y, sp. 1).
- Theaceae** (Y, gen. 9; T, gen. 9): *Adinandra* Jack (Y, spp. 9; T, spp. 2), *Anneslea* Wall. (Y, sp. 1; T, sp. 1), *Camellia* L. (Y, spp. 39; T, spp. 12), *Cleyera* Thunb. (T, sp. 1), *Eurya* Thunb. (Y, spp. 43; T, sp. 12), *Gordonia* J. Ellis (Y, spp. 4; T, sp. 1), *Pyrenaria* Blume (Y, spp. 6; T, sp. 1), *Schima* Reinw. (Y, spp. 8; T, sp. 1), *Stewartia* L. (Y, spp. 4), *Ternstroemia* Mut. (Y, spp. 6; T, sp. 1).
- Thymelaeaceae** (Y, gen. 7; T, gen. 3): *Aquilaria* Lam. (Y, sp. 1), *Daphne* L. (Y, spp. 18; T, spp. 3), *Edgeworthia* Meisn. (Y, spp. 3), *Erioseola* Blume (Y, sp. 1), *Rhamnoneuron* Gilg (Y, sp. 1), *Stellera* L. (Y, sp. 1; T, sp. 1), *Wikstroemia* Endl. (Y, spp. 14; T, spp. 5).
- Tiliaceae** (Y, gen. 7; T, gen. 4): *Berrya* Roxb. (T, sp. 1), *Burretiodendron* Rehd. (Y, spp. 3), *Colona* Cav. (Y, spp. 2), *Corchorus* L. (Y, spp. 4; T, spp. 3), *Grewia* L. (Y, spp. 15; T, spp. 4), *Microcos* L. (Y, spp. 2), *Tilia* L. (Y, spp. 8), *Triumfetta* L. (Y, spp. 4; T, spp. 4).
- Toricelliaceae** (Y, gen. 1): *Torricellia* DC. (Y, sp. 1).
- Trilliaceae** (Y, gen. 2; T, gen. 2): *Paris* L. (Y, spp. 11; T, sp. 1), *Trillium* L. (Y, sp. 1; T, sp. 1).
- Triuridaceae** (T, gen. 1): *Sciaphila* Blume (T, spp. 2).
- Trochodendraceae** (T, gen. 1): *Trochodendron* Sieb. & Zucc. (T, sp. 1).

Typhaceae (Y, gen. 2; T, gen. 2): *Sparganium* L. (Y, spp. 5; T, sp. 1), *Typha* L. (Y, spp. 3; T, spp. 2).

Ulmaceae (Y, gen. 6; T, gen. 5): *Aphananthe* Planch. (Y, spp. 2; T, sp. 1), *Celtis* L. (Y, spp. 11; T, spp. 5), *Gironniera* Gaudich. (Y, sp. 1), *Trema* Lour. (Y, spp. 5; T, spp. 3), *Ulmus* L. (Y, spp. 8; T, spp. 2), *Zelkova* Spach (Y, spp. 2; T, sp. 1).

Umbelliferae (Y, gen. 50; T, gen. 17): *Acronema* Falc. (Y, spp. 10), *Anethum* L. (Y, sp. 1), *Angelica* L. (Y, spp. 8; T, spp. 4), *Anthriscus* (Pers.) Hoffm. (Y, spp. 2), *Arcuatopterus* Shan & Sheh (Y, spp. 3), *Bupleurum* L. (Y, spp. 12; T, sp. 1), *Carum* L. (Y, sp. 1), *Centella* L. (Y, sp. 1; T, sp. 1), *Chaerophyllopsis* de Boissies (Y, sp. 1), *Chaerophyllum* L. (Y, sp. 1), *Chamaesium* H. Wolff (Y, spp. 6), *Cicuta* L. (Y, sp. 1), *Cnidium* Cuss. (Y, sp. 1; T, sp. 1), *Conioselinum* Hoffm. (T, sp. 1), *Coriandrum* L. (Y, sp. 1), *Cortia* DC. (Y, sp. 1), *Cryptotaenia* DC. (Y, sp. 1; T, sp. 1), *Cyclorhiza* M. L. Sheh & R. H. Shan (Y, spp. 2), *Daucus* L. (Y, sp. 1), *Dickinsia* Franch. (Y, sp. 1), *Eryngium* L. (Y, sp. 1; T, sp. 1), *Ferula* L. (Y, spp. 2), *Foeniculum* Mill. (Y, sp. 1), *Glehnia* F. Schmidt (T, sp. 1), *Haplosphaera* Hand.-Mazz. (Y, sp. 1), *Harrysmithia* H. Wolff (Y, sp. 1), *Heracleum* L. (Y, spp. 19), *Hydrocotyle* L. (Y, spp. 7; T, spp. 7), *Ligusticum* L. (Y, spp. 27), *Meeboldia* H. Wolff (Y, sp. 1), *Melanosciadium* H. Boissieu (Y, sp. 1), *Nothosmyrnium* Miq. (Y, sp. 1), *Notopterygium* H. Boissieu (Y, spp. 2), *Oenanthe* L. (Y, spp. 8; T, spp. 2), *Oreomyrrhis* Endl. (T, spp. 3), *Osmorhiza* Raf. (Y, sp. 1; T, sp. 1), *Ostericum* Hoffm. (Y, sp. 1), *Peucedanum* L. (Y, spp. 8; T, spp. 2), *Physospermopsis* H. Wolff (Y, spp. 6), *Pimpinella* L. (Y, spp. 28; T, spp. 2), *Pleurospermum* Hoffm. (Y, spp. 19), *Pternopetalum* Franch. (Y, spp. 17), *Sanicula* L. (Y, spp. 7; T, spp. 2), *Selinum* L. (Y, spp. 2), *Seseli* L. (Y, spp. 3), *Sinocarum* H. Wolff (Y, spp. 7), *Sinolimprichtia* H. Wolff (Y, sp. 1), *Sium* L. (T, sp. 1), *Tetrataenium* (DC.) Manden. (Y, spp. 2), *Tongoloa* H. Wolff (Y, spp. 7), *Torilis* Adans. (Y, spp. 2; T, spp. 2), *Trachydium* Lindl. (Y, spp. 7), *Trachyspermum* Link (Y, spp. 2), *Vicatia* DC. (Y, spp. 3).

Urticaceae (Y, gen. 19; T, gen. 21): *Boehmeria* Jacq. (Y, spp. 17; T, spp. 8), *Chamabainia* Wight (Y, sp. 1; T, sp. 1), *Cypholophus* Wedd. (T, sp. 1), *Debregeasia* Gaudich. (Y, spp. 5; T, sp. 1), *Dendrocnide* Miq. (T, spp. 2), *Droguetia* Gaudich. (Y, sp. 1), *Elatostema* J. R. Forst. & G. Forst. (Y, spp. 71; T, spp. 14), *Girardinia* Gaudich. (Y, spp. 2; T, sp. 1), *Gonostegia* Turcz. (T, spp. 3), *Laportea* Gaudich. (Y, spp. 5; T, spp. 2), *Lecanthus* Wedd. (Y, spp. 3; T, sp. 1), *Leucosyke* Zoll. & Moritsi (T, sp. 1), *Maoutia* Wedd. (Y, sp. 1; T, sp. 1), *Memoralis* (Benn.) Buch.-Ham. (Y, sp. 1), *Nanocnide* Blume (Y, sp. 1; T, sp. 1), *Oreocnide* Miq. (Y, spp. 7; T, spp. 2), *Pellionia* Gaudich. (Y, spp. 14; T, spp. 2), *Pilea* Lindl. (Y, spp. 43; T, spp. 13), *Pipturus* Wedd. (T, sp. 1), *Poikilospermum* Zipp. (Y, spp. 2; T, sp. 1), *Pouzolzia* Gaudich. (Y, spp. 6; T, spp. 2), *Procris* Comm. (Y, sp. 1; T, sp. 1), *Sarcochlamys* Gaudich. (Y, sp. 1), *Urtica* L. (Y, spp. 8; T, spp. 2).

Verbenaceae (Y, gen. 5; T, gen. 2): *Duranta* L. (Y, sp. 1), *Lantana* L. (Y, sp. 1; T, sp. 1), *Phyla* Lour. (Y, sp. 1; T, sp. 1), *Stachytarpheta* Vahl (Y, sp. 1), *Tsoongia* Merr. (Y, sp. 1).

Violaceae (Y, gen. 1; T, gen. 2): *Hybanthus* Jacq. (T, sp. 1), *Viola* L. (Y, spp. 58; T, spp. 13).

Vitaceae (Y, gen. 9; T, gen. 7): *Ampelocissus* Planch. (Y, spp. 3), *Ampelopsis* Michx. (Y, spp. 10; T, sp. 1), *Cayratia* Juss. (Y, spp. 12; T, spp. 2), *Cissus* L. (Y, spp. 14; T, spp. 5), *Leea* D. Royen (Y, spp. 7; T, spp. 2), *Parthenocissus* Planch. (Y, spp. 4; T, sp. 1), *Tetrastigma* (Miq.) Planch. (Y, spp. 32; T, spp. 4), *Vitis* L. (Y, spp. 12; T, spp. 4), *Yua* C. L. Li (Y, spp. 2).

Xyridaceae (Y, gen. 1; T, gen. 1): *Xyris* L. (Y, sp. 1; T, sp. 1).

Zannichelliaceae (Y, gen. 1; T, gen. 2): *Halodule* Endl. (T, spp. 2), *Zannichellia* L. (Y, sp. 1; T, sp. 1).

Zingiberaceae (Y, gen. 18; T, gen. 5): *Alpinia* Roxb. (Y, spp. 25; T, spp. 12), *Amomum* Roxb. (Y, spp. 26), *Boesenbergia* Kuntze (Y, spp. 3), *Caulokaempferia* Larsen (Y, sp. 1), *Cautleya* Hook. f. (Y, spp. 2), *Costus* L. (Y, spp. 5; T, sp. 1), *Curcuma* L. (Y, spp. 11), *Etlingera* Giseke (Y, spp. 2), *Globba* L. (Y, spp. 3), *Hedychium* J. Koenig (Y, spp. 16; T, sp. 1), *Kaempferia* L. (Y, spp. 3), *Paramomum* S. Q. Tong (Y, sp. 1), *Pommereschea* Wittm. (Y, spp. 2), *Rhynchanthus* Hook. f. (Y, sp. 1), *Roscoea* Sm. (Y, spp. 10), *Siliquamomum* Baill. (Y, sp. 1), *Stahlianthus* Kuntze (Y, spp. 2), *Vanoverberghia* Merr. (T, sp. 1), *Zingiber* Mill. (Y, spp. 25; T, spp. 4).

Zosteraceae (T, gen. 1): *Zostera* L. (T, sp. 1).

Zygophyllaceae (Y, gen. 1; T, gen. 1): *Tribulus* L. (Y, spp. 2; T, spp. 2).

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